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# THE ROLE OF MECHANICAL STRESSES IN BONE FORMATION IN VITRO

By A. GLUCKSMANN

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## INTRODUCTION

In animal experiments on the effect of mechanical conditions on skeletal development, it is almost impossible to define the minute stresses set up in skeletal tissue, as the physical conditions are so greatly complicated by the presence of muscles, nerves and blood supply. Moreover, there is evidence that mechanical stresses may have an indirect effect on the tissue by altering its blood supply and thereby its nutrition (Löschke & Weinnold, 1922; Leriche & Policard, 1928; Greig, 1931).

Many of these complicating factors can be eliminated by using the tissue culture method. Bone and cartilage can be grown in vitro in the absence of blood vessels, nerves and muscles, and the direct effect of various known stresses on the histological architecture of skeletal tissue can therefore be studied with much greater precision than is possible in vivo.

In earlier work (Glucksmann, 1938) it was found that a regular pattern could be imposed on irregularly formed osseous tissue in vitro by mechanical agents, and also that perichondrium and periosteum reacted to pressure stresses by forming cartilage both at the site of pressure and the site of displacement (Glucksmann, 1939). In the present investigation the effect of pressure and tension on cartilage and of tension on periosteum has been studied.

## MATERIAL AND METHODS

Skeletal tissue from chick embryos was grown by either the hanging-drop or watch-glass technique in a mixture of 1 drop of fowl plasma and 2 drops of extract of a 10-day chick embryo. The explants were transferred to fresh medium every 2–3 days. Each culture was either drawn or photographed at the beginning and end of the culture period.

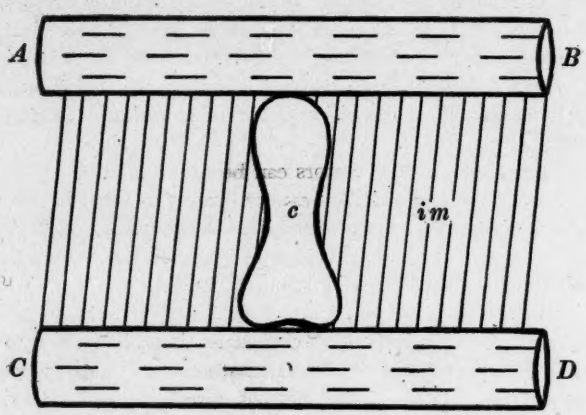
The cultures were fixed in Zenker's fluid or in Susa and when ossified were decalcified in formol-nitric acid. Serial sections were cut and stained with Azan, haematoxylin-eosin or by Wilder's method.

## RESULTS

### *The effect of pressure and tension on cartilage*

***Experimental conditions.*** Two methods of applying pressure and tension to cartilage were used; they have been described in detail elsewhere (Glucksmann, 1939).

(*a*) ***Direct application.*** The rudiment was implanted between a pair of 17-day embryonic ribs in culture. The ribs, which were connected by intercostal muscles, gradually drew together during cultivation, thus exerting pressure on the rudiment implanted between them on the surface of the muscle (Text-fig. 1). Plates of scleral cartilage from 11-day embryos, 4-day embryonic femora and tibiae, and 7–12-day embryonic metatarsals and phalanges were implanted in this way; thirty-two experiments were made.




Text-fig. 1. Diagram showing the experimental arrangement for the direct application of pressure to a cartilaginous rudiment. The rudiment (*c*) is placed on the intercostal muscle (*im*) between the two ribs (*AB* and *CD*). During the period of cultivation the ribs approach each other, thus exerting a pressure on the cartilaginous rudiment.

(*b*) ***Indirect application.*** Barriers were placed in the direction of expansion of the rudiment which thus had to grow against a resistance (Text-fig. 2). Four-day embryonic femora and tibiae and the metatarsals and phalanges of 7–12-day embryos were used both as experimental cartilages and as barriers. Fifty-four experiments were made.

The effect of both these methods is to bend or even break the growing cartilage. The convex side is thus subjected to tension and the concave side to pressure, so that the action of both types of stress can be considered together.

***Results.*** The degree of distortion produced depends on the type of cartilage and the duration of pressure. Scleral cartilage bends easily and usually breaks on the convex side by about the 6th day of cultivation, while 4-day embryonic femora and tibiae, though readily bent, seldom break. The metatarsals and

phalanges of older (7–12-day) embryos, which are usually covered by a thin osseous sheath, bend only slightly. As might be expected, curvature is greatest in the oldest cultures.

Evidence of pressure stresses on the concave and tension stresses on the convex side of the rudiment is seen as soon as bending begins and is expressed in an alteration of the arrangement of the cells, in the structure of the ground substance, and in the relationship between cells and ground substance. These changes increase with the curvature.

(*a*) *The arrangement of the cells.* On the concave side of the rudiment the long axes of the cells shift through 90° from a direction parallel with the surface. The cells also become pressed closely together (Pl. 1, fig. 1), and in very bent cartilage some degenerate (Pl. 1, fig. 4), while others are squeezed out into the surrounding tissue and may assume the appearance of fibroblasts. On the convex side the cells maintain their normal orientation but become flattened and more widely separated. If the bending is very great the cells either degenerate or are freed from their capsules.

When the curvature is slight, the cells in the interior of the cartilage are not affected, but as it increases their arrangement alters according to whether they lie nearer the concave or the convex surface of the rudiment. If the cartilage breaks under pressure the cells in the break degenerate and the neighbouring cells lose their orientation.

Text-fig. 2. Diagram showing the experimental arrangement for the indirect application of pressure to a growing rudiment. In this combination the two terminal 'barrier' rudiments prevent free longitudinal expansion of the middle rudiment and thus force it to bend.

These changes in cellular arrangement are only seen in those parts of the cartilage which are subjected to pressure and tension stresses; elsewhere in the rudiment the cells maintain their normal orientation (Pl. 1, figs. 1, 2, 3, 5).

(*b*) *Structure of the ground substance.* In response to pressure and tension, fibrils appear and the chondromucoid matrix disappears in the ground substance. In slightly bent cartilage, fibrils occur on or near the surface and lie parallel to the elongated cells; they are restricted to the intercapsular substance. When the curvature is great, the whole ground substance, including the capsules, and even intracapsular spaces left empty by the degeneration of

the enclosed cells, becomes fibrillar. This fibrillar system originates at the vertex of the concave surface (Pl. 1, figs. 2, 3), whence it runs into the interior and spreads fan-wise near the convex side so that the superficial fibres run parallel to the surface. The convex surface is pitted with shallow erosions (Pl. 1, fig. 5) lined with elongated cells, which are produced by dehiscence of the ground substance. The perichondrium is disrupted in this area.

When chondroblasts are squeezed out at the concave surface, the accompanying fibres are also extruded and may disappear in the surrounding mesenchyme, make contact with perichondrial fibres or, in ossifying regions, become continuous with bone or periosteal fibres (Pl. 1, fig. 4). This third condition is well seen when cartilage rods covered by a thin osseous coat are subjected to pressure. The bony sheath is folded in at the concave vertex (Pl. 1, fig. 2) and in very bent rudiments tends to break inside the cartilage (Pl. 1, fig. 3). The broken edges of the bone become the central points of attachment of the fibrillar system of the cartilage, and the bone and cartilage fibrils seem to be continuous.

As fibre formation progresses, the interfibrillar matrix of the ground substance disappears. Fibrillation does not appear in neighbouring parts of the rudiment not subjected to abnormal mechanical stresses, and its amount depends on the degree of stress applied, showing clearly that the fibrils are formed in direct response to the mechanical factors.

*Conclusion.* Pressure and tension exerted on cartilage in vitro cause the reorientation of the cells, the disintegration of the hyalin ground substance, and its replacement by a fibrillar system.

### *The effect of tension stresses on bone-forming tissue*

Three series of experiments were made and will be considered separately.

*Series* 1. The rudiments were bent by blocking their longitudinal expansion by terminal barriers (see p. 2 and Text-fig. 2). The tibiae and femora of 4-day embryos and the metatarsals and phalanges of 7–12-day embryos were used; fifty-four experiments were made.

Both the effect and the degree of bending depend on the degree of differentiation at the beginning of the experiment. Unossified rudiments from 4-day embryos bend much and form little or no bone on the convex side but an abnormally large amount on the concave surface (Pl. 1, fig. 5). On the other hand, the partly ossified rudiments from older embryos bend very slightly so that the hour-glass-shaped cartilage is rarely curved sufficiently to produce more than a flattening of one side instead of forming a strictly convex contour, and ossification is always greater on the 'convex' than on the concave side (Pl. 1, fig. 6).

This difference in the distribution of new bone between the younger and older rudiments is due to the difference in behaviour between perichondrium and periosteum. Perichondrium is readily detached from the cartilage, and,

as the rudiment bends, the membrane is drawn right away from the shaft on the concave side by the natural elasticity of the tissue. In the space thus formed between the perichondrium and the cartilage, tension lines are set up which radiate outwards from the vertex of the concave surface of the cartilage (Murray, 1936; Studitsky, 1934). Bone deposition follows these radiating tension lines, so that midway along the shaft the bone is orientated at right angles to the cartilage (Pl. 1, fig. 5). On the convex surface the perichondrium becomes very attenuated or even disrupted and shallow erosion cavities often appear in the cartilage.

The periosteum investing the older rudiments, however, is firmly attached to the osseous sheath encasing the shaft and therefore does not become drawn away from the concave side of the cartilage. The increased bone-formation on the convex side follows tension stresses running parallel with the surface of the cartilage (Pl. 1, fig. 6).

*Series* 2. In each experiment two or more rudiments were explanted parallel to each other and a short distance apart. They soon became enclosed in a common fibrous and later osseous capsule which gradually contracted during cultivation, thus drawing the rudiments towards each other and altering the direction of the tension stresses in the capsule (Text-fig. 3). The greatest contraction and consequent change in stress occurred during subcultivation when the centrifugal stresses of the plasma clot were released and no longer counteracted the forces pulling the rudiments together (Glucksmann, 1938, 1939). The object of the experiments was to study the effect of these changes of stress on the architecture of the newly formed bone.

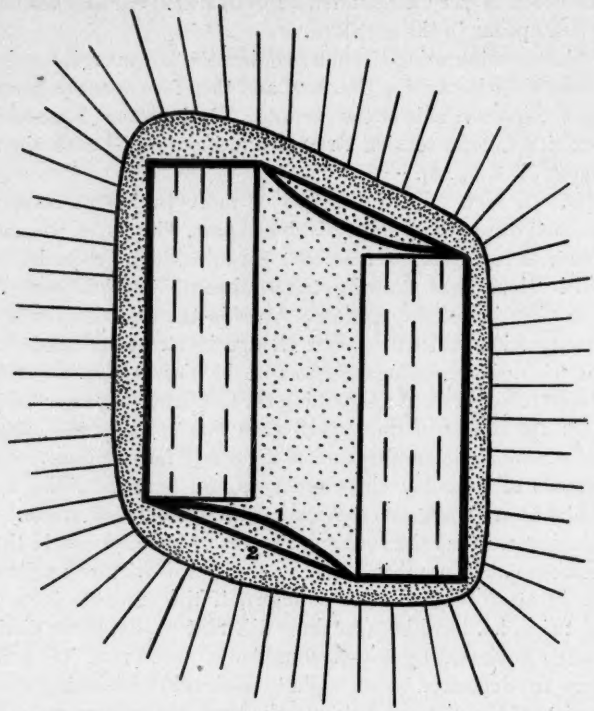
Metatarsals of 7–12-day chick embryos and parts of tibiae from 2-day hatched chicks were used; seventy-seven experiments were made.

Sections showed that the successive layers of bone formed in the common capsule correspond in number with the changes of culture medium, i.e. the periods of greatest tension. For example, if the explants have been subcultivated twice, i.e. have been in three different media, three distinct layers of bone, often separated by non-osseous tissue, are formed (Pl. 2, fig. 7). The three layers are deposited at an angle to each other according to the degree of contraction of the distance between the explanted rudiments.

*Series* 3. In this series of experiments the degree or direction of the normal tension stresses in the ossifying explant was altered by removing all or part of one epiphysis. The epiphyses expand in two directions, parallel to the long axis of the shaft and at right angles to it. Since the periosteal fibres are attached distally to the epiphyses, this expansion exerts tension stresses on the periosteum in two directions. Thus, by cutting off one epiphysis the lateral component of these forces is removed and the tension greatly reduced. When only half the epiphysis is removed the tension stresses are, of course, affected on one side only.

If tension promotes bone formation, then reducing the tension by excision of all or part of one epiphysis might be expected to reduce ossification. The

results of fourteen such experiments, in which phalanges and metatarsals of 10–12 day chick embryos were used, showed that this is true. Removal of one complete epiphysis greatly reduces the amount of bone deposited round the diaphysis (Pl. 2, fig. 8). When half the epiphysis is cut off, no bone develops on the operated side of the rudiment, but on the intact side ossification is normal (Pl. 2, fig. 9). In cases where less than half the epiphysis was removed, bone formation proceeded normally on the intact side. On the operated side




Text-fig. 3. Diagram showing two distinct layers (1 and 2) in an osseous capsule enclosing two bone rudiments. The inner layer became bent when the distance between the original explants contracted during subcultivation.

bone was not deposited on the surface of the diaphysial cartilage in the usual way but developed in the superficial periosteal tissue in a region which was subjected to tension stresses in the capsule formed around a prominent part of the diaphysis (Pl. 2, fig. 10).

*Conclusion.* (1) Tension stresses promote bone formation in osteogenic tissue in vitro.

(2) The histological structure of developing bone in vitro is orientated along the lines of tension in the osteogenic tissue.

## DISCUSSION

It has been shown in earlier work that pressure applied to perichondrium or periosteum in vitro causes the disappearance of collagen fibres and the formation of cartilage. In the present experiments it was found that both pressure and tension applied to differentiated cartilage produce the reverse effect, viz. the disintegration of the hyaline matrix and its replacement by fibrillar tissue. It can hardly be assumed that the mechanical stresses merely mask or unmask pre-existing fibres by causing the deposition or resorption of interfibrillar matrix. In the first place the fibres of perichondrium or periosteum subjected to pressure actually disintegrate during cartilage formation; in the second place, in cartilage subjected to pressure fibres appear even in empty *intracapsular* spaces where they were obviously not pre-existent.

Weiss (1933) suggested that the micellae of intercellular substance tend to become transformed into a more stable fibrillar structure if the mechanical conditions remain fairly constant. It is possible that, when perichondrium or periosteum is transformed into cartilage in response to mechanical factors, the fibres are reduced to a micellar structure and the micellae become impregnated with chondromucoid matrix. Conversely, pressure and tension stresses may lead to the orientation of the micellae in the differentiated cartilage, to the formation of fibres along the pressure and tension lines, and to their separation from and the resorption of the chondromucoid matrix.

The results described above indicate that tension stresses affect the development of the osseous architecture by determining where bone shall be laid down in the osteogenic tissue. As shown elsewhere, young differentiated bone also responds to mechanical conditions in vitro so that an irregular structure may be forced into a regular pattern by pressure stresses.

Thus mechanical factors influence the structure of bone in vitro both during its formation and after it has differentiated. They also influence the amount of bone which is formed in any given region since, as described above, increasing the normal tension of the periosteum also increases bone formation, while reducing the tension correspondingly diminishes ossification.

The effects of mechanical stresses on the development of skeletal tissue which have been observed in vitro are not peculiar to tissue culture conditions, and similar results have been obtained in vivo by other workers. For example, when early bone rudiments are grafted on the chorio-allantoic membranes of fowl eggs (Murray, 1936; Studitsky, 1934) some of the grafts become very bent. In these bent rudiments bone formation is increased on the concave side and follows the radiating lines of tension set up between the cartilaginous shaft and the detached perichondrium just as in the bent explants in vitro. If half-bone rudiments are grafted, only a thin veil of bone is formed, whereas grafts of entire rudiments ossify almost normally (Murray, 1936); this result agrees with that obtained in vitro when an entire epiphysis is removed at the time of explantation. In experiments on fractures in dogs, Krompecher (1937)

showed that in callus, as in cultures of osteogenic tissue, tension stresses promote direct bone formation while pressure initiates cartilage formation, but if the pressure persists the cartilage disintegrates and is replaced by bone.

It is clear, therefore, that the effect of mechanical stresses on skeletal tissue developing under the extremely simplified conditions of culture in vitro are essentially the same as those produced by similar mechanical factors on skeletal tissue developing in vivo where the situation is complicated by the presence of muscles, blood vessels and nerves. This affords evidence that many of the structural effects resulting from mechanical stresses in vivo are due to the direct action of the stresses on the skeletal tissue itself.

## SUMMARY

1. Pressure and tension stresses exerted on cartilage in vitro cause the reorientation of the cartilage cells and lead to the disintegration of the hyaline ground substance and its replacement by a fibrillar system.

2. Tension stresses promote bone formation in osteogenic tissue in vitro and determine the pattern of osseous architecture.

3. Skeletal tissue cultivated in vitro responds directly to mechanical stresses.

I have pleasure in acknowledging my indebtedness to Dr H. B. Fell for her very helpful advice and criticism, to Mr V. C. Norfield for the drawing of the diagrams, and to Mr G. Lenny for the photomicrographs.

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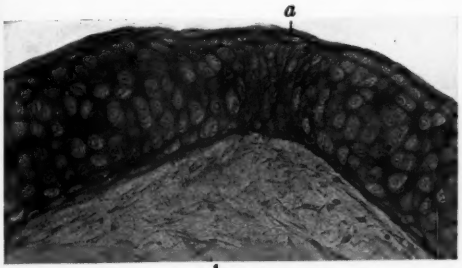
## EXPLANATION OF PLATES 1 AND 2

### Plate 1

Fig. 1. Section through a culture of scleral cartilage from an 11-day chick embryo, implanted between the ribs from a 17-day chick embryo and cultivated by the hanging-drop-method for 6 days. ×270. Azan. The cartilage cells are compressed at the curvature. Cells at the convex surface are flattened (*a*), while on the concave side the long axis of the cells is shifted through 90° from a direction parallel with the surface.

Fig. 2. Section through the metatarsal of an 11-day chick embryo cultivated with two barrier rudiments for 8 days by the watch-glass technique. ×155. Azan. Note the cellular arrangement, the folding in of the osseous sheath (*o.s.*) and the appearance of a fibrillar system originating on the concave surface.

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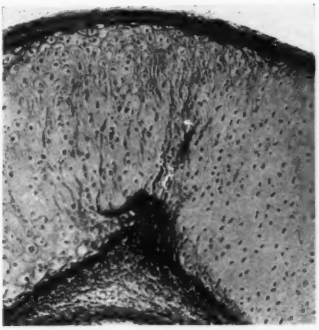

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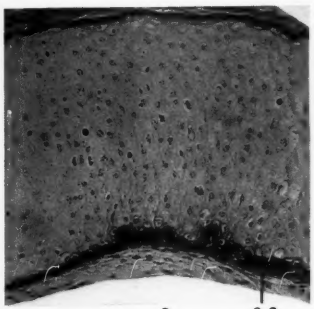


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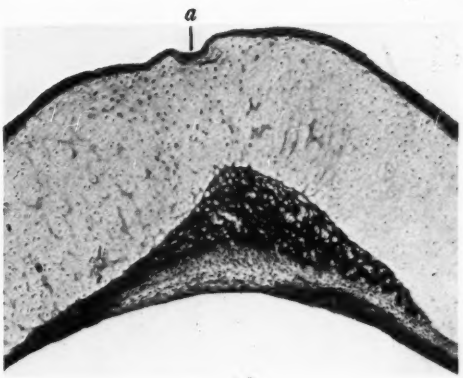


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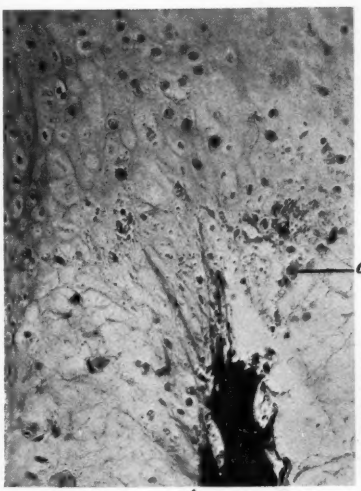


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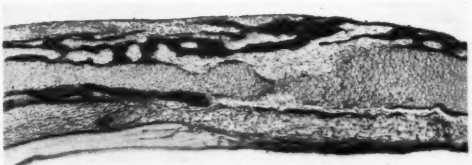

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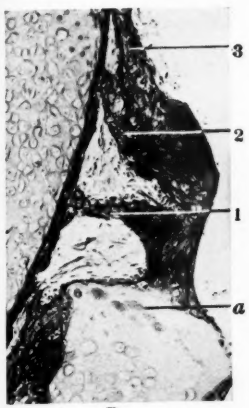


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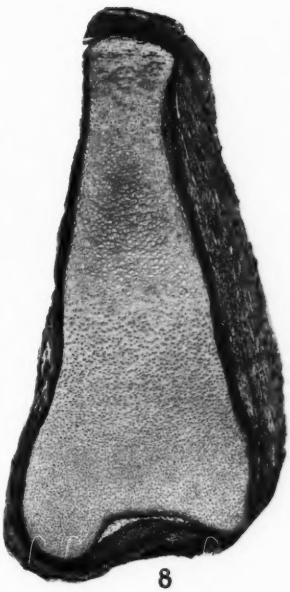

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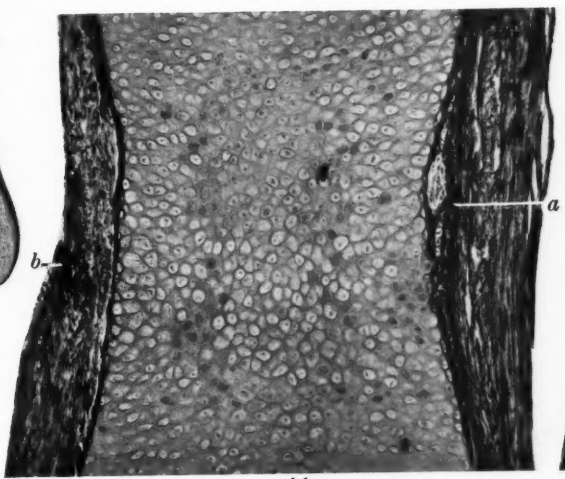


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**Fig. 3.** Section through a metatarsal of a 10-day chick embryo cultivated with two barrier rudiments for 10 days by the watch-glass technique. ×95. Azan. The folded in osseous sheath is broken and the broken edges form the central points of attachment of the fibrillar system in the cartilage.

**Fig. 4.** Section through a femur of a 4-day chick embryo implanted between the ribs of a 17-day chick embryo, cultivated by the watch-glass technique for 11 days. ×270. Azan. The cartilage fibres are continuous with bone fibrils and periosteal fibres. At (*a*) degenerate cartilage cells are seen.

**Fig. 5.** Section through a metatarsal cultivated in combination with phalanges of the same 7-day chick embryo by the watch-glass technique for 12 days. ×90. Azan. The convex surface of the cartilage is pitted with shallow erosions (*a*). On the concave side bone formation is increased. The bone trabeculae are radiating outwards from the vertex of the curvature.

**Fig. 6.** Section through a metatarsal cultivated in combination with phalanges from the same 11-day chick embryo by the watch-glass technique for 8 days. ×40. Azan. Bone formation is increased on the convex surface. The newly-formed bone runs parallel with the surface of the cartilage.

PLATE 2

**Fig. 7.** Section through a combination of parts of an 11-day metatarsal cultivated by the hanging-drop method for 9 days. ×150. Wilder-carmalum-light green. Three successive layers (1, 2, 3) are seen in the osseous capsule corresponding to two subcultivations, i.e. cultivation on three culture media. Note intracapsular fibres formed in spaces vacated by degenerating cartilage cells (*a*).

**Fig. 8.** Section through a phalanx from an 11-day chick embryo cultivated by the watch-glass technique for 10 days. ×50. Wilder-carmalum-light green. The upper epiphysis has been removed. The amount of bone formation on both sides of the diaphysis is reduced.

**Fig. 9.** Section through the phalanx from an 11-day chick embryo cultivated by the watch-glass method for 10 days. ×90. Wilder-carmalum-light green. The right half of the upper epiphysis has been removed in an oblique line. There is no bone formation on the right side of the diaphysis while on the left side ossification has proceeded.

**Figs. 10, 11, 12.** Section through the phalanx from an 11-day chick embryo cultivated by the watch-glass technique for 8 days. Wilder-Azan. ×30 (Fig. 10), ×130 (Fig. 11), ×265 (Fig. 12). Only the left half of the upper epiphysis has been removed. Normal bone formation (*a*) has occurred on the right side of the diaphysis. On the left side bone (*b*) has been formed on the margin of the culture but not immediately adjacent to the diaphysis. Note the difference in density and arrangement of the periosteal tissue on the left and right side.

# THE BIFURCATION OF THE POSTERIOR CAVAL CHANNEL IN THE EUTHERIAN FOETAL HEART

By E. C. AMOROSO,[1] A. E. BARCLAY,[2]
K. J. FRANKLIN[2] and M. M. L. PRICHARD[2]

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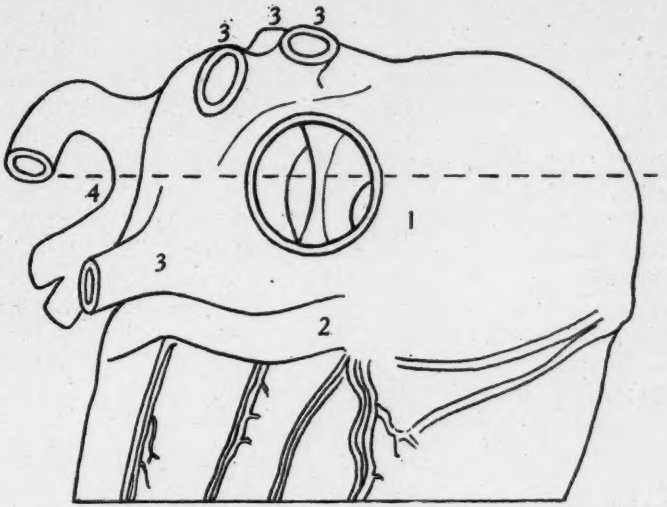
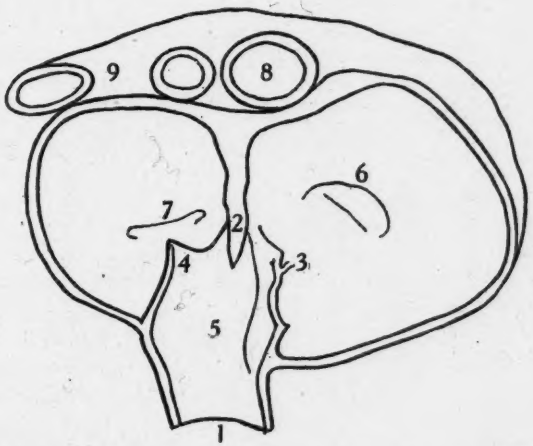
In 1939 Barclay *et al.* published results of the first direct studies of the circulation in intact foetuses. The subjects were nearly full-term lambs, delivered by Caesarean section; the technique used for recording was direct and indirect X-ray cinematography (Barclay *et al.* 1940), combined with intravascular injections of radio-opaque substances. The findings agreed, in so far as they overlapped, with results obtained by other methods (Barclay *et al.* 1941), and, for our present purpose, the essential results were as follows. The anterior caval inflow passes in its entirety to the right atrium and right ventricle. The posterior caval inflow, on the other hand, divides. The larger part, estimated by us as being about three-quarters of the whole, passes by way of the foramen ovale to the left atrium and left ventricle; the smaller part passes to the right atrium and right ventricle.

With these experimental findings to stimulate us, we proceeded to study and to define the structural features that are concerned in the division of the posterior caval stream. In so doing, we felt ourselves compelled to propose a new functional nomenclature (see Amoroso *et al.* 1941) for certain parts of the foetal heart and great vessels, and one of the new terms that we suggested was 'posterior caval channel'. In this we include not only the lumen of the posterior vena cava itself, but also the intracardiac continuation of the channel up to the levels at which the posterior caval blood discharges into the atrial cavities, for the stream does not divide until it has gone well into the heart, and thereafter its left and right divisions proceed still farther before they come into contact with other blood streams entering the atria. On the left side, the posterior caval blood has to pass beyond the valve of the foramen ovale; on the right side, it has to pass beyond the Eustachian valve (in those animals that possess this structure). Figs. 1 and 2, which are outline drawings made from two illustrations in Ziegenspeck (1905), may usefully be consulted at this point. Actually, as we shall see later, the ridge on which the posterior caval stream divides is so far within the heart that one must remove the posterior vena cava completely to get a good view, or photograph, of the ridge. So, to give the dynamic picture of the main afferent blood stream rushing up into the

[1] Royal Veterinary College. [2] Nuffield Institute.




Text-fig. 1. Outline drawing from part of Fig. 1 in Ziegenspeck (1905). Heart of a 54 cm. long newborn child seen from behind. The interrupted line shows the line of section for the production of Text-fig. 2. Original legend: 1, inferior vena cava with limbus Vieussenii and valve of foramen ovale. 2, coronary sinus. 3, 3, 3, pulmonary veins. 4, pulmonary artery and ductus arteriosus.




Text-fig. 2. Outline drawing from Fig. 2 in Ziegenspeck (1905), showing view towards apex of heart revealed by cut along interrupted line in Text-fig. 1. Original legend: 1, inferior vena cava. 2, septum atriorum and limbus Vieussenii. 3, Eustachian valve. 4, valve of foramen ovale. 5, recess: remains of sinus venosus. 6, right ostium venosum. 7, left ostium venosum. 8, bulbus arteriosus. 9, pulmonary artery.

foetal heart and dividing, one must have some such inclusive term as our 'posterior caval channel'. The use of the term does not, of course, imply that the functional intracardiac continuation is embryologically of similar origin to the posterior vena cava itself. Later on we hope to give a fuller account of the channel in various genera; our more immediate object in this paper is to describe and to depict its bifurcation within the eutherian foetal heart, for this bifurcation is one of the key-points to the understanding of the foetal circulation.

We give below an abstract of the views of some of our predecessors, together with a summary of some of our own findings. The abstract is necessarily somewhat long, for no similar survey exists, and certain of the earlier writers deserve credit for what they accomplished even though, so far as we can judge, they failed to convince any great number of their contemporaries. One of the main reasons for their failures is that they had no experimental findings to adduce in support of their anatomical observations. In this respect we ourselves are more fortunate.

## PREVIOUS WORK

The foramen ovale, which is the left terminal division only of our posterior caval channel, was first described by Galen in the second century A.D., and thereafter it received considerable attention from anatomists in the second half of the sixteenth, and early part of the seventeenth, century. Thus there was a bias towards the consideration of one particular part of our channel, and away from the consideration of the channel as a whole, at the time when Harvey was preparing to publish his new doctrine of the circulation. In his book (see Franklin, 1941) he included the first account of the foetal circulation, but this account was to some extent an interpolation by way of illustration, and in addition Harvey produced it by superimposing his new idea of the blood flow upon the anatomical data already extant about the foetal cardiovascular system. Further, Harvey's single 'vena cava' included both our present venae cavae and he did not, in his description of the foetal circulation, differentiate the ascending and descending branches of the vessel. So, on the one hand, the bias that we have mentioned was continued and, on the other hand, Harvey did not give his view of the course of the posterior caval stream, as separate from the anterior caval stream.

Richard Lower (1669, pp. 48–50, 54–6, and Pl. I, figs. 2, 3. See Franklin, 1932; Franklin *et al.* 1940, pp. 80–2) recognized two venae cavae and it seems, from a careful examination of his description and figures, that he envisaged a division of the inferior caval stream, the larger part going by way of the foramen ovale to the left atrium and the rest to the right atrium, while the superior caval blood went to the right side only. But Lower included in his account one error of commission (he made his 'tubercle' greater in man than in lower animals) and one of omission, and in consequence the influence that he might have exerted was in large measure nullified.

Haller, in his various summaries of his own findings and of those of his predecessors, arrived at a surprisingly accurate idea of the course of the blood flow through the foetal heart. By his time, too, the Eustachian valve had definitely come into the picture, for the foetal cardiovascular system that was most studied was the human one, and the valve had been pictured and described in a number of publications in the first half of the eighteenth century. But Haller, through Lower's error of commission and his own predilection for human material, was sceptical about the existence of the intervenous tubercle and, perhaps through the same predilection combined with his too intimate study of previous work, he did not reach the concept of a posterior caval channel with the foramen ovale as its left terminal division.

The man who did actually initiate the more correct outlook was C. F. Wolff, though, in so doing, he included in his inferior vena cava parts that, as we now know, do not developmentally belong to it, i.e. his inferior vena cava was our posterior caval channel. His important communication on the foramen ovale and its function in directing the blood movement was made to the Imperial Academy of Sciences in St Petersburg in January 1776 and was published later in the same year. As a result of his anatomical studies, Wolff concluded that the human foetal auricles were not in direct communication with one another, but that the inferior vena cava was interposed between them, and had independent openings into each of them. The isthmus of Vieussens was common to both right and left openings, which were completed by the Eustachian valve and the valve of the foramen ovale respectively. The isthmus was nearer the right than the left side, and Wolff estimated that, towards full term, about two-thirds of the inferior caval blood would take the left-hand route, and about one-third the right-hand one. He also examined the heart of the foetal calf. In this there was no Eustachian valve, and there were certain other differences from the human. But here again the isthmus of Vieussens divided the inferior vena cava, which terminated in short right and left branches. The bifurcation was even visible on the external surface of the preparation.

Despite its essential rightness, Wolff's contribution appears to have met with more opposition than praise, and to have been without effect upon the bulk of contemporary opinion. Kilian (1826), in fact, stated that it was scarcely known at all to physiologists and anatomists, the only definite supporters that he could cite being Okel, Meckel, and Louron.

Kilian himself, who also worked in Russia, stated that the inferior vena cava opens into both left and right auricles, the two openings being halves of one and the same channel. His views were repeated in 1834 by his pupil Knabbe, who produced the longest review that at present exists of the literature upon the foetal cardiovascular system and circulation. Unfortunately, Kilian linked up his anatomical findings with a new, and not generally acceptable, hypothesis of the foetal circulation, and neither his nor Knabbe's contribution seems to have had a wide public.

When, however, Ziegenspeck began work under Preyer towards the end of the century, Preyer gave him Knabbe's thesis to read, and Ziegenspeck was thereby referred to Wolff's communication. He began his own researches by confirming Wolff's concept in a number of guinea-pig foetuses, and later he proved it true also in a long series of human foetuses (Ziegenspeck, 1882, 1884, 1905). Further, he produced drawings (1905, Figs. 1–4) that made his points perfectly clear. He realized, in the light of embryological research, that morphologically part of Wolff's inferior vena cava was cardiac in origin, even if the functional picture was not thereby altered. But, like Kilian, he invented a complicated and unsatisfactory hypothesis of the foetal circulation to accompany his correct anatomical findings and, so far as one can judge, his views did not gain many adherents.

It is obvious from the literature that even true statements about the foetal cardiovascular system are liable to be ineffective when unsupported by experimental findings about the foetal circulation, Such experimental work on living foetuses was begun by Pohlman (1909), but, as we have stated, it was not until 1939 that the first results of direct studies on intact foetuses became available.

## PERSONAL OBSERVATIONS

These direct studies were confined to one genus (*Ovis*) and should, for obvious reasons, be extended to others. There are, however, technical reasons limiting the number of genera suitable for study, and in addition the war has imposed various restrictions upon experimental work. We have, therefore, examined carefully the gross anatomy of the foetal lamb and have correlated, in respect of its cardiovascular system, the main structural and functional findings.

We have, further, made an extensive comparative study of all the eutherian foetal material that we have been able to obtain, in order to see if, in these various other animals, there are present the anatomical features that we regard as important in the foetal lamb. The number of foetuses that we have so far examined is well over a hundred, and they have included representatives of over a score of genera from the orders Ungulata, Cetacea, Carnivora, and Primates. Ziegenspeck, as we have noted, examined representatives of Rodentia.

The essential anatomical features have been present in every foetus studied by us, so there is some justification for supposing that in eutherian foetuses as a whole the circulation may proceed much in the same way as we have found it to do in our foetal lambs. At all events, such a possibility is not at once contraindicated by departures from a general plan in the structure of the foetal heart and great vessels.

Of all the anatomical features the most important, in our view, is the bifurcation within the heart, into left and right terminal divisions, of the posterior caval channel. The bifurcation occurs on what has been variously

termed the isthmus or limbus of Vieussens or annulus ovalis or isthmus atriorum, and it is essential, for the correct appreciation of the foetal circulation, that this bifurcation should be generally recognized.

The proper initial procedure is to look up through the posterior vena cava (see Ziegenspeck, 1905, Fig. 1, or our Text-fig. 1, which is a simplification of it). One then sees very clearly what must happen to the blood stream passing up this vessel in the living foetus. We have verified the correctness of Ziegenspeck's drawing by photographs of our own human specimens, and we reproduce one of these photographs as Pl. 1, fig. 3. Pl. 1, figs. 4–6 are similar views in sheep, horse and ox foetuses. Pl. 1, fig. 7 is a closer view of the bifurcation in another foetal horse—in it can also be seen part of the valve of the foramen ovale and the line of its attached border, which only in part corresponds with the isthmus of Vieussens; the opening of the coronary sinus, valveless in this as in many other genera, is also visible. Pl. 1, fig. 8 is a view of the heart and lungs of a foetal lamb, divided by a transverse cut made just cranial to the bifurcation of the posterior caval channel—it shows the two terminal divisions of the channel, which discharge into the left atrium and right atrium respectively. Finally, in Pl. 1, fig. 9, we show the bifurcation as revealed by a longitudinal cut made from right to left through the heart and lungs of a horse foetus.

We hope that by our survey of the subject, and by these photographs (which are but a selection from the many that we have taken), we may finally eliminate the bias that originated in pre-Harveian times and that has, in general, continued to the present day. In other words, we hope that we may establish our concept of a functional 'posterior caval channel' bifurcating, within the eutherian foetal heart, into left and right terminal divisions. For such a concept is in accordance with the experimental findings and interprets structure, as it should be interpreted in connexion with the foetal circulation, in terms of function.

For the ridge upon which the posterior caval stream divides we have already (Amoroso *et al.* 1941) suggested the term 'crista dividens'.[1] The term 'isthmus' is an unsatisfactory one, as Haller early (1763, p. 38) pointed out; so also, however, is Haller's own 'annulus fossae ovalis', for our connotation of 'fossa ovalis' is more limited than his, and the ring, as he himself acknowledged, is incomplete.

## SUMMARY

The 'posterior caval channel' in the eutherian foetus bifurcates into left and right terminal divisions, through which the posterior caval blood passes to the left atrium and right atrium respectively. The prominent ridge at the

[1] We have since received the objection that 'crest', in ordinary English, does not have the meaning required. According to the Oxford English Dictionary, however, the anatomical definition of 'crest' is not inappropriate in the present connexion, and in any case we could use the term 'dividing ridge' as the English rendering of 'crista dividens'. If, however, an alternative is required, we would suggest the name 'carina dividens', for the bifurcation of the posterior caval channel results in the reproduction of a central ridge not unlike the 'carina tracheae'.

line of bifurcation has been inappropriately styled, in the past, 'isthmus of Vieussens', 'annulus fossae ovalis', and so forth. We ourselves prefer the term 'crista dividens', *anglice* 'dividing ridge', which is not only short but also indicative of the experimentally determined function of the structure.

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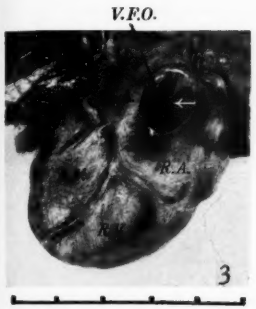
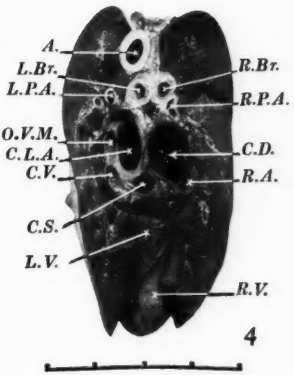
## EXPLANATION OF PLATE 1

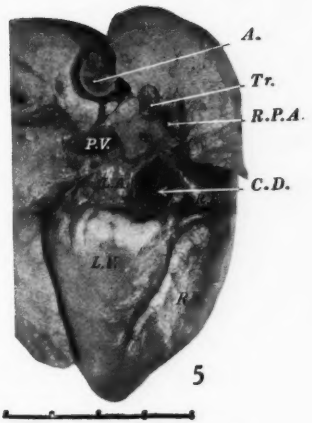
Fig. 3. Human foetus, 8½ months. Diaphragmatic view of heart and part of lungs to show dividing ridge, *C.D.*, of inferior caval channel. Inferior vena cava itself removed. *R.A.*, *L.A.*, right and left atria. *V.F.O.*, part of valve of foramen ovale. *R.V.*, *L.V.*, right and left ventricles. Centimetre scale.

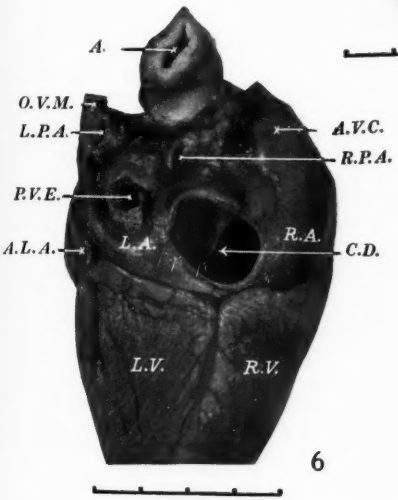
Fig. 4. Lamb, 2 days after birth. View, looking cranially, of heart and lungs transected to show dividing ridge, *C.D.*, of posterior caval channel. *R.A.*, right atrium. *C.L.A.*, cavity of left atrium. *C.S.*, coronary sinus. *C.V.*, coronary vein. *O.V.M.*, oblique vein of Marshall (main azygos drainage in this genus). *R.V.*, *L.V.*, right and left ventricles. *R.P.A.*, *L.P.A.*, right and left pulmonary arteries. *A.*, aorta. *R.Br.*, *L.Br.*, right and left main bronchi. Centimetre scale.

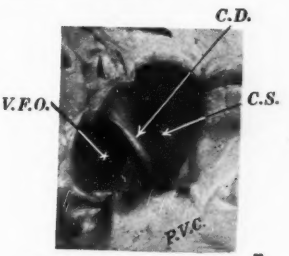
Fig. 5. Horse foetus, 5½ months. View, looking cranially, of heart and lungs, the latter transected somewhat obliquely, to show dividing ridge, *C.D.*, of posterior caval channel. Posterior vena cava itself removed. *R.A.*, *L.A.*, right and left atria. *P.V.*, large pulmonary vein. *R.V.*, *L.V.*, right and left ventricles. *R.P.A.*, right pulmonary artery. *A.*, aorta. *Tr.*, trachea. Centimetre scale.

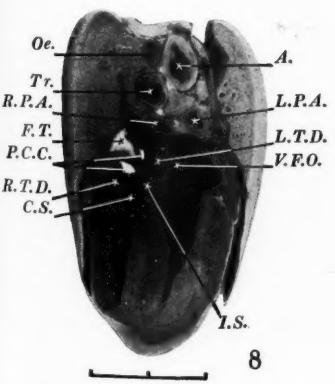


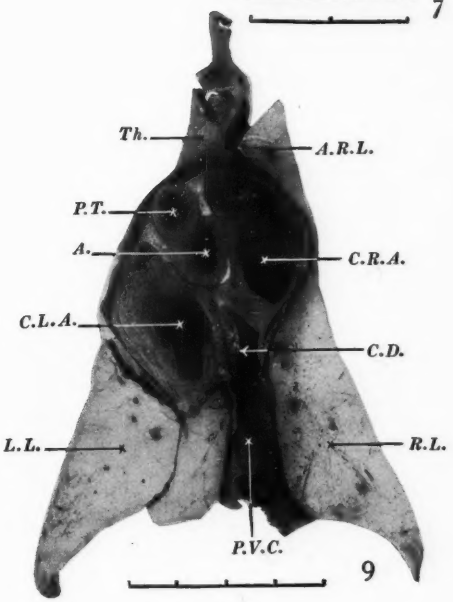




AMOROSO AND OTHERS—Posterior caval channel of foetus

Fig. 6. Ox foetus, about 5 months. Diaphragmatic view of heart, with posterior vena cava removed, to show dividing ridge, *C.D.*, of posterior caval channel. *R.A.*, *L.A.*, *A.L.A.*, right and left atria, and auricle of left atrium. *A.V.C.*, anterior vena cava. *O.V.M.*, oblique vein of Marshall (main azygos drainage in this genus). *P.V.E.*, pulmonary vein entry. *R.V.*, *L.V.*, right and left ventricles. *R.P.A.*, *L.P.A.*, right and left pulmonary arteries. *A.*, aorta. Centimetre scale.

Fig. 7. Horse foetus, fairly mature. Closer, somewhat lateral, view of posterior caval channel, and dividing ridge, *C.D.* *P.V.C.*, posterior vena cava slit open to expose dividing ridge, etc. *C.S.*, opening (valveless) of coronary sinus. *V.F.O.*, valve of foramen ovale. Centimetre scale.

Fig. 8. Sheep foetus, about 120 days. View, looking caudally, of heart and lungs transected just cranial to bifurcation of posterior caval channel, *P.C.C.*, showing its right, *R.T.D.*, and left, *L.T.D.*, terminal divisions. *V.F.O.*, part of valve of foramen ovale. *C.S.*, opening (valveless) of coronary sinus. *F.T.*, fatty tissue lying dorsal to intercaval 'tubercle' (see Lower, 1669, 48). *I.S.*, interatrial septum just cranial to dividing ridge of *P.C.C.* *R.P.A.*, *L.P.A.*, right and left pulmonary arteries. *A.*, aorta. *Tr.*, trachea. *Oe.*, oesophagus. Centimetre scale.

Fig. 9. Horse foetus, 200 + days. View, towards sternum, revealed by a longitudinal cut from right to left through lungs and heart. *R.L.*, *A.R.L.*, *L.L.*, right lung, apex of right lung, left lung. *P.V.C.*, posterior vena cava. *C.D.*, dividing ridge of posterior caval channel. *C.R.A.*, *C.L.A.*, cavities of right and left atria. *P.T.*, pulmonary trunk. *A.*, aorta. *Th.*, thymus. Centimetre scale.

# THE NERVE SUPPLY OF THE BRANCHIAL ARCH ARTERIES IN *VIPERA BERUS*

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A number of investigators (Ask-Upmark, 1935; Muratori, 1937; Boyd, 1934, 1937; and others) have produced evidence supporting Koch's (1931) thesis that persistent portions, in the adult, of the embryonic branchial arch pattern are sites of election for the development of specialized pressor-receptor nerve endings. Most of the material studied by these workers has been mammalian and avian, and, apart from incomplete reports on elasmobranchs (Boyd, 1936) and Amphibia (Eloff, 1935; Boyd, 1933), there has been no full investigation of the afferent nerve endings and fibres in the great vessels of the lower vertebrates. The present contribution is based on the study of a complete series of sections through the anterior end of an adult viper (*Vipera berus*). The specimen, which extends to the caudal end of the heart, was impregnated, before sectioning, with the de Castro modification of the Cajal silver technique.

The Ophidia are highly specialized, and the elongation of the neck region with the associated caudal migration of the heart has resulted in marked modifications of the branchial arch arterial pattern, with disappearance of one of the common carotid arteries and a wide separation of the vessels derived from the third and fourth embryonic arterial arches. These modifications, however, do not disturb the fundamental relations of the persisting vessels and, indeed, by the separation of the vessels they enable the nerve supplies to be studied more readily, and with less opportunity for confusion than in other types. Further, since the time of the classical contributions of Rathke to the problem of branchial arch arterial pattern, the main features in the developmental history of the ophidian carotid, aortic and pulmonary arch arteries have been well established and there can be no reasonable doubt about the 'arch' value of any of the vessels which are to be considered.

In the viper the third branchial arch arteries in the course of their development show the considerable changes characteristic of the Ophidia in general. The ductus caroticus of each side disappears and the definitive vascular pattern shows the blood supply to the carotid system arising from the right systemic arch artery (which receives oxygenated blood from the left portion of the ventricle) by a single trunk usually called the primary carotid (*arteria carotis primaria* of Rathke). This vessel soon gives off a branch to the thyroid gland (see Figs. 3, 6), which possibly represents the remnant of the caudal portion of the right common carotid artery, and then swings to the left, passing behind the left thymus complex, and continues anteriorly as a vessel which is

obviously the persisting left common carotid artery. It represents the caudal portion of the left common carotid artery. Rathke called it the *arteria carotis communis*, but O'Donoghue's (1912) term, left common carotid, is to be preferred as it emphasizes the embryological significance of the vessel.[1]

Beyond the upper lobe of the thymus the left common carotid artery passes along the left side of the oesophagus and trachea, giving off medially directed branches until it reaches the posterior region of the head where it divides into the left internal and external carotid arteries. By way of large transverse anastomoses between these branches and the corresponding vessels of the opposite side of the head the right carotid system receives its blood supply (see Fig. 1) and, notwithstanding the absence of a right common carotid artery, the cephalic portion of the right carotid system shows a degree of development identical with that of the left side.

The commencement of the left internal carotid artery and of the equivalent vessel of the right side shows a slight dilatation and a thickened adventitial cuff of connective tissue. In the walls of each of these vessels, and in the surrounding connective tissue, there are to be found a number of stellate pigmented cells. Among these pigmented cells are a number of ramifying nerve fibres which, for the most part, terminate in the wall of the vessel by endings which are only slightly branched. In this feature the fibres differ markedly from the extensive ramifications of the endings found in the carotid sinus and equivalent regions of birds and mammals. The morphological position of the dilatation and the small extensions of the lumen of the internal carotid artery into the thickened wall of the vessel, however, present a picture which is very similar to that shown by the carotid sinus region of mammalian embryos. In the viper the nerve fibres which terminate in the endings found in the internal carotid artery are derived from the vagal trunk; in mammals, as is now well known, most of the fibres to the carotid sinus and carotid body are of glossopharyngeal origin, but a few come from the vagus nerve. In all the Ophidia, however, the connexions between the vagus and glossopharyngeal nerves are very intimate and the vagal origin of the fibres to the third arch artery is probably to be explained by the assimilation of fibres which are morphologically of glossopharyngeal origin into the course of the upper portion of the vagus trunk.

Palme (1934) gave a brief description of the nerve supply to the internal carotid artery of the emerald lizard, basing his account on material impreg-

[1] Incidentally, it may be stated here that no structure, on either side, could be found which might represent the ligamentum caroticum described by Brandt (1865) in *N. natrix* and *V. berus*. Both Hochstetter (1902) and O'Donoghue (1917) have reported their inability to find this ligamentous vestige of the embryonic ductus caroticus. Neither of them, however, appears to have studied sections, but depended, like Brandt himself, on dissections. As my sections are serial it appears unlikely that the ligamentous band described by Brandt could be missed and it can therefore be stated that the ligamentum caroticum is not constantly present in the viper. From the developmental history of the neck region in snakes, indeed, it would be surprising if it ever persists, for the elongation of the neck and the caudal migration of the heart are the very factors which appear to be of importance in its disappearance in other types.

nated by the Bielschowsky technique. Van Bemmelen (1886) described the resemblance shown by the commencement of the internal carotid artery of lizards, particularly young specimens, to the carotid labyrinth of Amphibia, and Palme also refers to this resemblance in his Azan-stained material. The latter writes: 'In the emerald lizard the carotid artery shows a sac-like dilatation at its bifurcation. The vessel wall at many points is thickened and projects

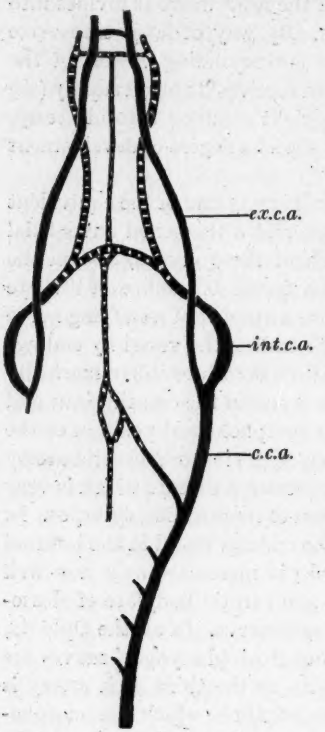


Fig. 1.

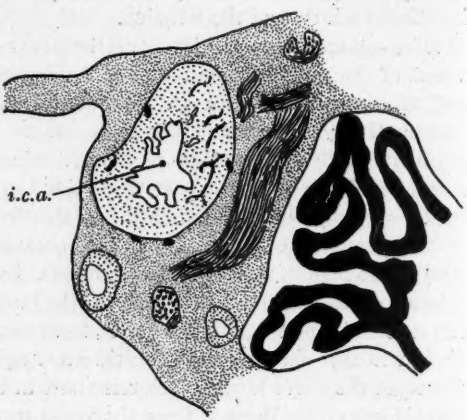


Fig. 2.

Fig. 1. Diagram of the carotid system of *Vipera berus*. *c.c.a.* left common carotid artery; *int.c.a.* internal carotid artery; *ex.c.a.* left external carotid artery. The intracranial and intraspinal vessels are represented by interrupted lines.

Fig. 2. Camera lucida drawing of the right internal carotid artery (*i.c.a.*) to show the thickened adventitia, the irregularities of the lumen and the nerve fibres in the wall.

into the lumen producing diverticulae (Ausbruchtungen) and the appearance of labyrinth formation. In the surrounding adventitia many branching black pigment cells are to be found.' After stressing the resemblance between this appearance and that found in the carotid labyrinth (gland or body) of the frog, Palme adds: 'In the adventitia collections of paraganglionic cells are to be found, especially at those points where the swellings of the carotid wall are

thickest. These paraganglionic cells frequently lie in small groups between the processes of the pigment cells so that there may be difficulty in distinguishing them. They are, apparently "chromierbar" and in the Bielschowsky material they show deep black granulations. Between the cell groups a rich network of fine nerve fibres is found branching in the adventitia of this segment of the vessel wall. The type of endings cannot be determined in the available material.'

It is obvious from this account that Palme's findings in the emerald lizard are very similar to those described above for the viper. In the latter it has not been found possible to identify with certainty the paraganglionic cells. No cells which could be taken to be identical with those found in the mammalian carotid body can be found, but related to the nerve endings (and occasionally to the pigmented cells) there are rounded cells with a pale-staining cytoplasm which are probably equivalent to those described by Palme. Cells similar to those described by Palme had been described much earlier by Trinci (1912) in relation to the walls of the carotid, aortic and pulmonary vessels of *Gongylus ocellatus*, *Lacerta muralis*, *Uromastix spinipes* and *Anguis fragilis*. These cells were taken by Trinci to be homologous with the adrenal chromaffin cells, and he called them, collectively, the cardiaco-cervical chromaffin bodies. He stressed the fact, however, that they have very variable degrees of chromaffinity according to the species studied. More recently, Adams (1939) has also called attention to these cells in the adventitia of the carotid arch, at the point of origin of the internal carotid artery, in *Lacerta* (species not named). Adams also draws attention to the numerous pigmented cells in relation to these 'paraganglionic' cells, and he states that he observed very fine branches of the superior laryngeal nerve passing to this region. These cells will obviously be of importance in any attempt to throw light on the problem of the cells of the carotid and similar bodies of mammals and birds. In these vertebrate groups there is still no completely satisfactory statement on their nature. Some workers (Kohn, 1900, and his school; Trinci, 1912; Kose, 1907) have taken them to be identical in nature and origin with the adrenal medullary cells; others (e.g. Watzka, 1937) consider them to stand in the same relation to the cranial parasympathetic system as do the adrenal chromaffin cells to the sympathetic system. Both of these attitudes accept the cells as paraganglionic in nature. Meijling (1928) has described them as modified sensory ganglionic cells and attributes to them Nissl bodies and neurofibrillae. Schumacher (1938) takes them to be modified 'Quellzellen', of vessel wall origin, and equivalent to those found in the walls of arterio-venous anastomoses. Goormaghtigh & Pannier (1939) have considered them to be partly paraganglionic and partly of 'Quellzellen' origin. Nonidez (1935, 1937) has avoided committing himself as to their origin, calling them sometimes 'epithelioid', sometimes 'epithelial', cells, but he does not consider it likely that they are paraganglionic in nature. In my own investigations on the development of the human carotid body (1937) I was unable to persuade myself that all of the so-called paraganglionic cells in it are derived from the glossopharyngeal, vagus and

sympathetic trunks. For the cells from these sources migrate into the carotid body at comparatively late stages, and, in sections stained with the usual routine techniques, cannot be distinguished from the cells of the large perivascular mesenchymal cuff which surrounds the commencement of the embryonic internal carotid artery. Until more definite evidence on the precise origin and histogenesis of these cells is available it seems more satisfactory to use a non-committal term for them. *Glomus* cells or *epithelioid* cells are, at present, more satisfactory as terms of reference for them than *paraganglionic* cells. The first two terms have already been extensively used in the literature and they do not prejudice the issue of the real nature and origin of the cells, a prejudice which is inevitable when the word paraganglion is used.

Leaving as undetermined, then, the nature of the cells described by Trinci, Palme and Adams in the neighbourhood of the commencement of the reptilian internal carotid artery, the presence of the thickening in the wall of the artery, and of the nerve endings in and around this thickening, enables one to state that the reptilian third arch arteries have a specialized nervous apparatus associated with them. These vessels are equivalent, morphologically, not only to the mammalian carotid sinus region but also to the amphibian internal carotid artery with its specialized carotid labyrinth. The latter has a nerve supply from the glossopharyngeal nerve (Boyd, 1933) and is the site of origin of pressor reflexes (Meyer, 1927) and respiratory reflexes (Smith, 1939). It appears, then, that the reptilian condition may well be an intermediate stage, both morphologically and functionally, between the amphibian carotid labyrinth mechanism and the mammalian carotid sinus—carotid body apparatus. The deformation of the lumen of the internal carotid artery in the viper does not appear to be so pronounced as Palme found it in his lizard material, but the position and nervous connexions of the thickened segment of the internal carotid artery are so similar in these two reptiles that there can be no doubt of their equivalence.

Fig. 3, which is based on a graphic reconstruction, shows the aortic and pulmonary arch arteries of the viper. The right aortic arch arises from the left side of the ventricle, passes anteriorly behind the left aortic arch and pulmonary arch vessels, and then swings backwards to the right of the oesophagus and trachea to become the right portion of the dorsal aorta. In its course it gives off the large left common carotid artery, which has already been described, and the vertebral artery. The restriction of these large branches to the right aortic arch (for the corresponding left vessel has no considerable branches) is to be correlated with the fact that the right aortic arch, from the position of its origin, is in a favoured position for receiving oxygenated blood from the ventricle. The left aortic arch arises from the right side of the ventricle, its origin lying behind and slightly to the left of the commencement of the pulmonary trunk. It passes anteriorly, lying ventral to the right aortic arch vessel, and then swings dorsally to the left of the oesophagus and trachea. It gives off no large branches.

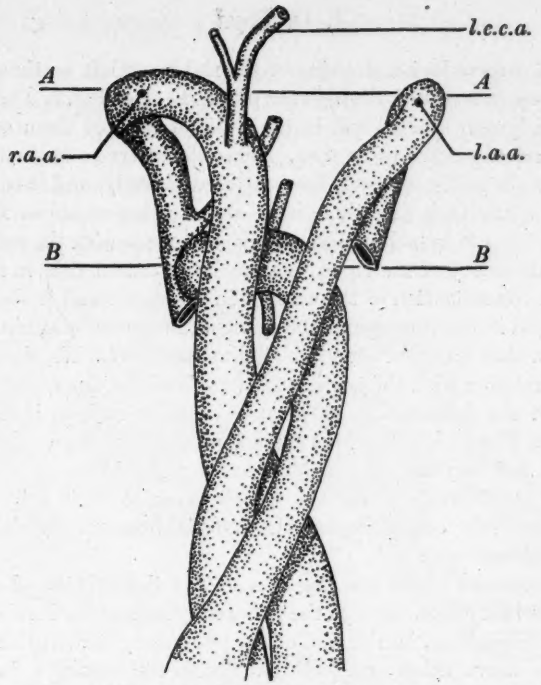


Fig. 3. Reconstruction of the right and left aortic arches and the pulmonary artery in *Vipera berus*. *l.c.c.a.* left common carotid artery; *r.a.a.* right aortic arch; *l.a.a.* left aortic arch; *A—A*, plane of section in Fig. 4; *B—B*, plane of section in Fig. 5.

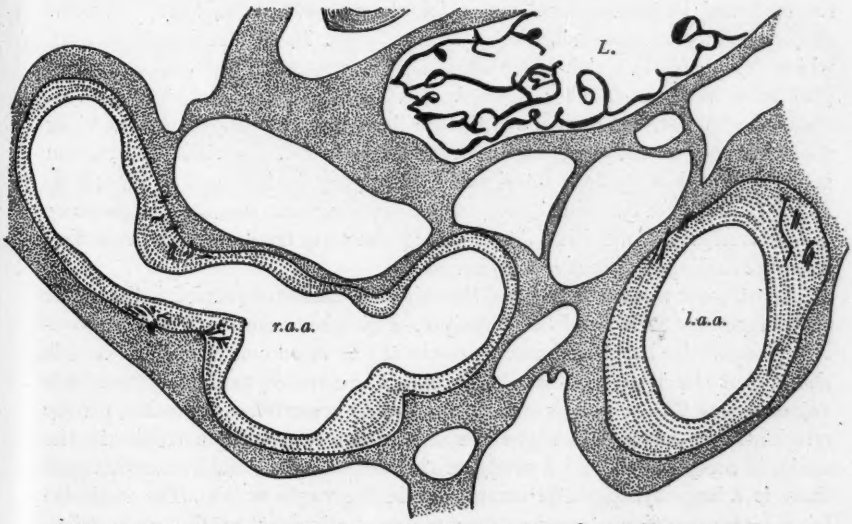


Fig. 4. Camera lucida drawing of a section to show position of nerve fibres and endings in the walls of the aortic arches. *L.* lung.

Fig. 4 is a camera lucida drawing of the right and left aortic arch vessels as they are seen in a section through the plane *A*—*A* of Fig. 3. The vessels are lying in large lymph spaces, and in the walls of each of them at this level numerous nerve fibres are to be seen. Nerve fibres are to be found at other levels in the walls of these vessels but scattered sparsely, and it is only at the apex of each aortic arch that there is a concentration of fibres. The endings in the vessel walls are branching but, as is also the case with the endings in the internal carotid artery of the viper, to a much less extent than in mammalian material. The concentration of the endings in the vessel wall is also much less than that found in the corresponding regions of mammals and birds, and it is less, too, than that found in the viper's pulmonary arch. No pigmented cells are found in relation with the aortic arch vessels of the viper, and there is no appearance of the deformation of the vessel lumina such as is found in the carotid region. There are cells of the epithelioid variety lying in the adventitia of the vessels, but they are not restricted to the region of the apex of the arch, being found at intervals along the vessels back to their origin from the ventricle. As with the carotid region, the material does not permit of a proper assessment of these cells.

Fig. 5 is a camera lucida drawing of a section through the plane *B*—*B* of Fig. 3. This section passes through the pulmonary arch at the level of its dorsal swing to the single lung. In the wall of the pulmonary arch at this level there are numerous nerve fibres and endings. The fibres terminate in a manner identical with the endings in the aortic arch vessels; in the pulmonary arch, however, they are much more numerous and extend over a much longer stretch of the vessel than in the aortic arches. This is in marked contrast with the results found in the mammal where (Nonidez, 1937; Boyd, 1941) very few sensory endings are found in the pulmonary trunk. In view of the recent work which demonstrates a rich nerve supply to the mammalian ductus arteriosus (Takino & Watanabe, 1938; Kennedy & Clark, 1941; Nonidez, 1941; Boyd, 1941), the thin fibrous remnant of the left ligamentum arteriosum of the viper was examined for nerve endings but none were found. The right ligamentum arteriosum appears to have retrogressed completely for it cannot be identified. In the condition of the lumen, the absence of pigmented cells, and the presence of scattered groups of epithelioid cells, the pulmonary trunk shows no variation from the findings in the aortic arch vessels.

An attempt was made to trace the origin of the fibres supplying the aortic and pulmonary arch vessels of the viper. Fig. 6 is based on a graphic reconstruction of the heart and main vessels of the specimen examined, and it shows that the fibres can, for the most part, be traced to the right and left vagus nerves. The results, however, can only be regarded as tentative, for the relationship between the vagus nerves and the sympathetic trunks in the snake is complicated, and a study of the sections gives the impression that there is a large sympathetic component in the vagus trunks. The vagi also have large ganglionic masses, presumably equivalent to the mammalian

ganglion nodosum, at the level of the vessels concerned, and some of these ganglia are separated from the main trunk of the nerve and make it impossible to be certain of their proper nature in adult material. As a first approximation, however, it is believed that the reconstruction presented in Fig. 6 shows the essential relationships. The right and left aortic arch arteries receive their supply from the corresponding vagus nerves, the branches coming off from the nerves in the neighbourhood of the vessels and not arising from the laryngeal

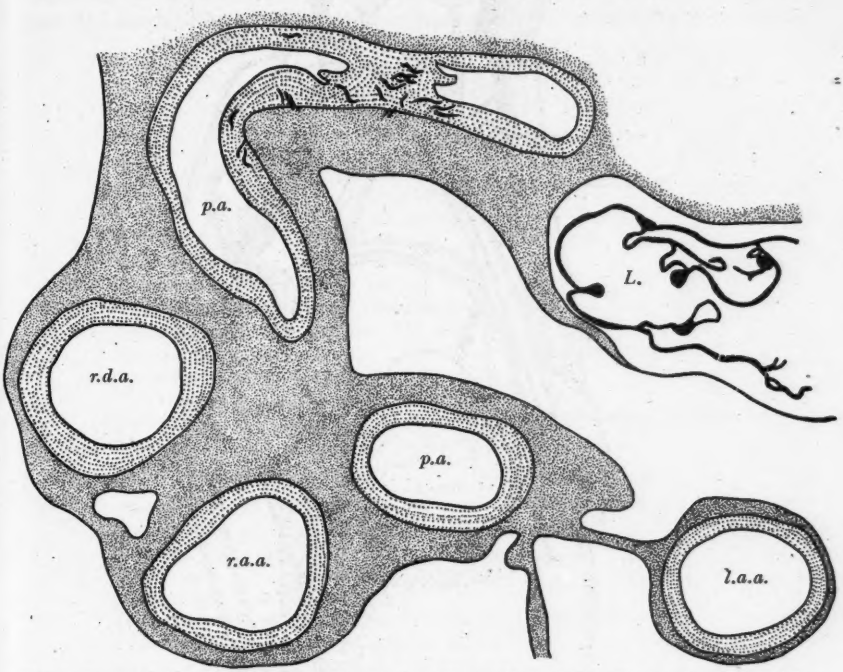


Fig. 5. Camera lucida drawing of a section to show the position of nerve fibres and endings in the walls of the pulmonary arch (*p.a.*). *r.a.a.* right ascending aorta; *r.d.a.* right descending aorta; *l.a.a.* left descending aorta.

nerves. These arterial branches are associated at their origin with branches which pass to the heart along the main trunks of the arteries and which also give off twigs to the vessels in their course. The left vagus nerve gives the main supply to the pulmonary artery, but this vessel does receive some branches from the right vagus. It is curious that the left vagus nerve should have almost monopolized the supply to the pulmonary arch, but it is possibly of significance that, in the specimen examined, it is the left ductus arteriosus which has persisted as the ligamentum arteriosum, the corresponding embryonic vessel of the right side having left no trace.

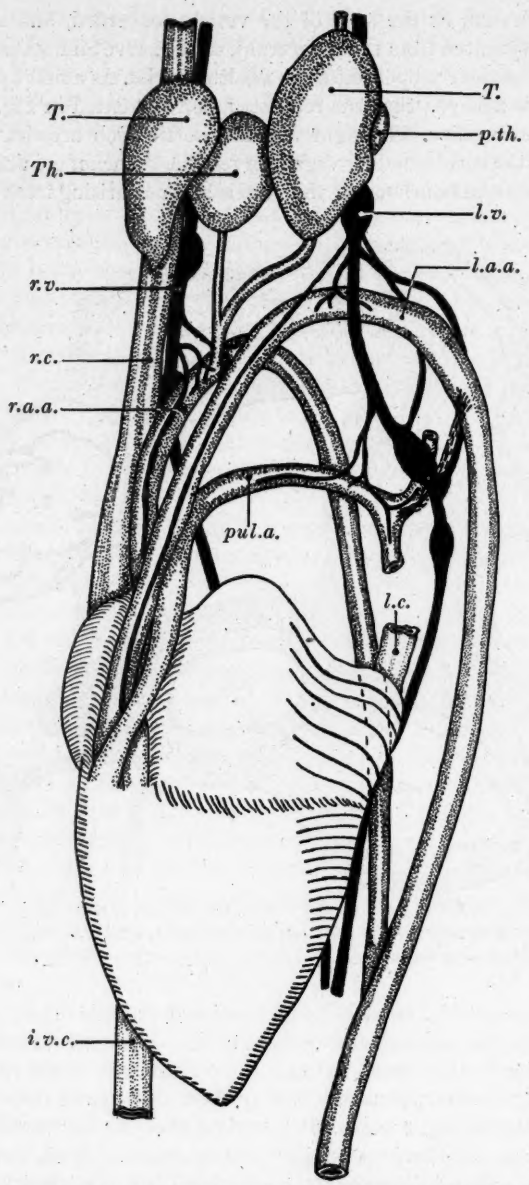


Fig. 6. Reconstruction of the heart and great vessels in *Vipera berus* seen from left side. *T.* thymus gland; *Th.* thyroid gland; *p.th.* parathyroid gland; *r.v.*, *l.v.* right and left vagus nerves; *r.c.*, *l.c.* right and left superior venae cavae; *i.v.c.* inferior vena cava; *pul.a.* pulmonary artery; *r.a.a.*, *l.a.a.* right and left aortic arches.

## SUMMARY

The nerve supply to the persistent portions of the branchial arch arteries in the adult viper is described. The internal carotid arteries, the aortic arches, and the pulmonary arch artery all possess an afferent innervation comparable with that found in the corresponding vessels of mammals and birds. The internal carotid artery, at its commencement, shows modifications which suggest that it may represent a transitional stage between the amphibian carotid labyrinth and the mammalian carotid body—carotid sinus complex.


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# MATRICES OF THE FACIALIS MUSCULATURE: HOMOLOGIZATION OF THE MUSCULATURE IN MONOTREMES WITH THAT OF MARSUPIALS AND PLACENTALS

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Huber summarized the views of comparative anatomists on the monotreme facialis musculature when he said: 'Although there are notable differences in *Echidna* and *Ornithorhynchus*, the arrangement of their facial muscles can be derived from a common ground-plan, which is peculiar to the monotremes and fundamentally different from the marsupio-placental ground-plan (Huber, 1930*b*, p. 142).

At the time this was written several hypotheses about the matrices of the facialis[1] musculature were current. Gegenbauer had suggested reptilian matrices. Ruge held that the platysma was the matrix for most of the facialis musculature; the sphincter colli (profundus) he thought was the matrix of certain of the deeper facialis muscles, e.g. the orbicularis oris and caninus. Afterwards he accepted Huber's modification, viz. that the platysma was the matrix of a comparatively small number of the facialis muscles, and that the majority were derived from the sphincter colli profundus. Much of his work was an advocacy of this, but evidence for the derivation of the caudo-rostral facialis muscles from this ventro-dorsal matrix was unconvincing.[2]

Another hypothesis was that of Boas & Paulli: 'That various facial muscles had taken origin independently of one another from indifferent mesoblastic elements in connection with the developments of the eyelids, the lips, the external nose etc.' (Boas & Paulli, 1908, p. 24). Recently Edgeworth has revived this: 'It (the superficial facialis musculature) is of late development, has no homologue in lower groups and originated within the mammalian phylum' (Edgeworth, 1935, p. 242). The Mm. digastricus posterior and stylo-

[1] The term facialis musculature denotes all the musculature innervated by the viith cranial nerve, whether this be cervical as in Selachians, Amphibia and Reptilia, or cervical and facial as in Mammalia. The term facial emphasizes only one portion of this distribution and is unsuited to the sub-Mammalia.

[2] This was based upon the conditions found in the cat and the dog, in which there was a fusion or an interlacement between some of the caudal fibres of the M. auriculo-labialis and some of the P. intermedia of the sphincter colli profundus (Huber, 1922, pp. 41–2). These inconsiderable connexions are exceptional; they seldom, if ever, are found in other mammals; they do not occur in marsupials. In working out his theory he sought to apply to the branches of the viith cranial nerve the muscle-nerve theory enunciated by Gegenbauer. So far the investigation of the nucleus of the viith cranial nerve has not been detailed enough to warrant this.

hyoideus he does not include with the above. This idea of a spontaneous generation of muscles is not easy to accept.

Still another hypothesis was put forward by Lightoller (1939). To this the conditions found in monotremes seem to give support: and, complementally, the hypothesis seems to explain the monotreme facialis musculature and to align it with that of marsupials and placentals.

*Reptilia.*[1] According to this hypothesis the reptilian facialis musculature is in two sheets, a superficial and a deeper; each of these is subdivided into dorsal and ventral portions. The superficial sheet consists of a dorsal P. noto-gnathica (*csd*1*c*) and a ventral P. mandibularis (*csv*1*c*); the deeper sheet of a dorsal P. cephalo-gnathica (*cL*2) and a ventral P. interhyoidea (*csv*2*a*). The P. cephalo-gnathica consists of two muscle masses, the P. epiphyoidea (*csd*2*a*) and the second levator (*L*2); these may be fused or incompletely separated[2] (Fig. 1A). Both components of the superficial group end in the subcutaneous tissues of the facial and intermandibular areas; some fibres may gain a deeper attachment, e.g. to the mandible. The dorsal components of the deeper group gain attachment to the post-articular process of the lower jaw; the ventral component to the hyoid.[3]

In the superficial group the dorsal P. noto-gnathica always passes superficial to the ventral P. mandibularis; in the deeper group the two dorsal components may lie in the same plane, or the P. epihyoidea may lie superficial to the second levator. They are often fused.

*Mammalian homologues.* These four muscle masses form the hypothesized matrices of the marsupio-placental facialis musculature. The P. noto-gnathica becomes the noto-platysma, the P. mandibularis the sphincter colli profundus—from which is derived the trachelo-platysma (Lightoller, 1940). Few, if any, of the other facial muscles are derived from this superficial group (Fig. 1B).

With the formation of the new squamo-dentary articulation and the disappearance of the post-articular process of the mandible, the P. cephalo-gnathica loses its ventral area of attachment; it surges forward into the facial area (Fig. 1 C, D), passing over the vertex as well as ventrally. In extant mammals certain 'rests' remain in the retro-auricular or cervical region which retain the original dorsal attachment of the P. cephalo-gnathica (*cL*2). By their mode of origin in this region muscles derived from the P. epihyoidea

[1] The reptilian musculature has previously been homologized with that of Selachians (Lightoller, 1940, inter alia). The selection, in the present article, of the reptilian musculature as the basis from which the matrices may be traced is not intended to imply that the Reptilia, or any other extant orders, are in the direct line of man's progenitors. Existence to-day implies a high degree of specialization which has removed them all far from the parent stem. But, alongside this, primitive characters of the original stock remain. It is such indicators, when identifiable, that are of value in visualizing and reconstructing primitive orders; to those belong the facialis group of muscles.

[2] The Pp. noto-gnathica and epihyoidea take origin in the middle line of the neck; the second levator chiefly from the skull.

[3] This forms the M. stylohyoideus in all mammals, including the monotremes, and will not require further mention.

(*csd2a*) can be distinguished from derivatives of the second levator (*L2*), despite the fact that each of these muscles subdivide into a superficial horizontal and a deeper transverse layer (Fig. 1 E, F). The superficial fibres in each case have an oblique caudo-rostral direction; the deeper fibres form large fans whose fibres are dorso-ventral, with rostral and caudal inclinations at their

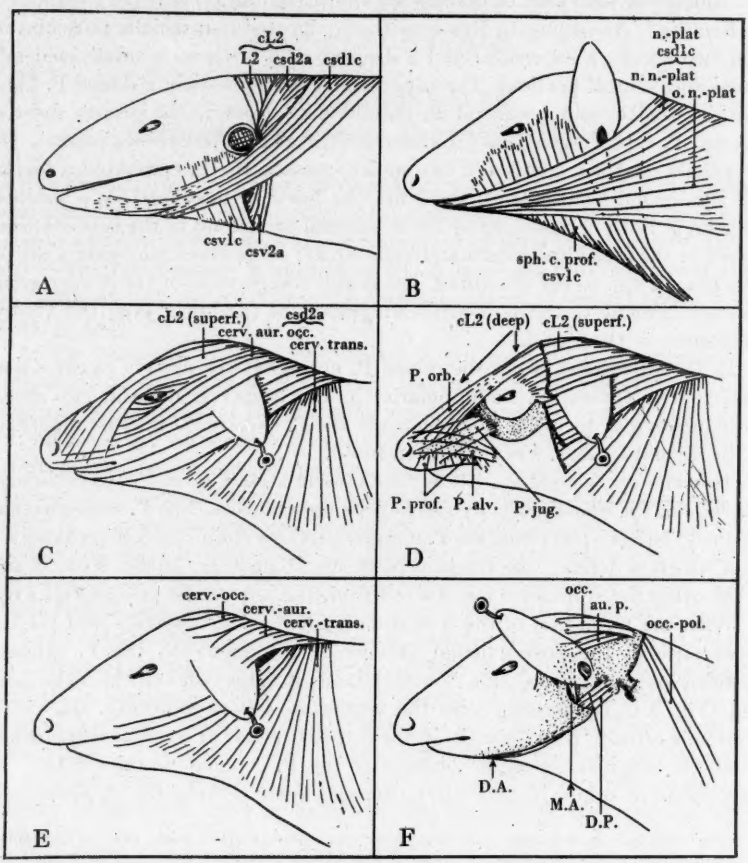


Fig. 1.

(For the legends of the text-figures, see p. 268.)

margins. These large fans are seldom, if ever, complete in any animal. The P. epihyoidea (*csd2a*) gives rise to the Mm. cervico-occipitalis, cervico-auricularis and cervicalis transversus; derivatives of the second levator (*L2*) are the Mm. occipitalis, auricularis posterior, mandibulo-auricularis (a variant), digastricus posterior and occipito-pollacalis (Fig. 1 E, F).

In the facial (pre-auricular) region no distinction can be drawn between the derivatives of the P. epihyoidea and the second levator, although superficial and deeper groups of muscles are to be found there (Fig. 1 C, D).

In the facial, as in the retro-auricular region, the primitive muscle sheets tend to split into layers or into individual and discrete muscles. This subdivision seems to depend either upon the degree of specialization acquired by some organ or upon the height of the phylogenetic family tree, e.g. in the subprimates the nose and ear muscles are highly developed, in the primates they are feeble. The converse holds for the collective facial musculature which reaches its highest differentiation in man.

*Monotreme facialis musculature.*[1] The description of this will be based upon the last hypothesis: only muscles innervated by the viith will be described. After removal of the skin two large muscle sheets are seen in each monotreme. Dorsally there is a powerful sheet whose fibres run obliquely caudo-rostrally: ventrally a large sheet whose fibres run ventro-dorsally and pass superficial to the above.

A. *Ventral sheet.* This is not the simple sphincter it appears to be. It is not the sphincter colli profundus, for, in the facial region of marsupials and placentals, this sheet always passes deep to the noto-platysma; just as, in Reptilia, the P. mandibularis passes deep to the P. noto-gnathica.[2] All the sphincter fibres in *Ornithorhynchus* and the majority in *Echidna* pass superficial to the platysmo-cervico-auricularis; for this reason it is usually called the sphincter colli superficialis—a term that is facile rather than explanatory. Apart from monotremes and rodents, a superficial transverse sheet of muscle is rare in the gular region; when it is present it is feeble, as in the dog. But in rodents there is a very powerful superficial sphincter sheet in this region; it is derived from the sphincter colli profundus and has been called the sphincter transitus (Lightoller, 1940). Many authors have called this sheet the sphincter colli superficialis, but the term sphincter transitus is preferable, and it is unambiguous. It is, now, suggested that the sphincter sheet of monotremes is homologous with the sphincter transitus of rodents.

A sphincter colli profundus, also, appears to be present, but its represen-

[1] The present series of dissections confirms those of Ruge, though he and Huber omit to mention the large M. cervicalis transversus (cranio-humeralis) in *Echidna*. There was no confirmation of the extensive 'limb portions of the facialis musculature' figured by Huber and described by him as though they were peculiar to monotremes (Huber, 1930*b*). They consist of (*a*) the *hd* and *hv'* muscles of Ruge. These are innervated by spinal nerves; (*b*) the omohyoideal fibres of the platysmo-cervico-auricularis. In many mammals, including the apes, these are well developed; in marsupials they may reach the forearm; (*c*) the M. cervicalis transversus. This is innervated by the viith, but its connexion with the limb is fortuitous and inconstant. The M. occipito-pollacalis of bats is analogous to but not homologous with these fibres.

[2] In the region of the neck the relationship between the sphincter colli profundus and platysma is less strictly followed. Here the fibres of the sphincter colli profundus may pass superficial to the platysma. These fibres are usually, and from the viewpoint of the present hypothesis wrongly, called the sphincter primitivus; they are a caudal (post-auricular) extension of the sphincter sheet.

tation in each genus is different (Figs. 2A, 4E). In *Echidna* the caudal fibres of the sphincter sheet pass deep to the platysmo-cervico-auricularis complex;[1] they, probably, represent the remains of the sphincter colli profundus. In *Ornithorhynchus* this facialis muscle (Fig. 4E) is well developed and lies deep to the sphincter transitus; it has retained reptilian characteristics which have masked

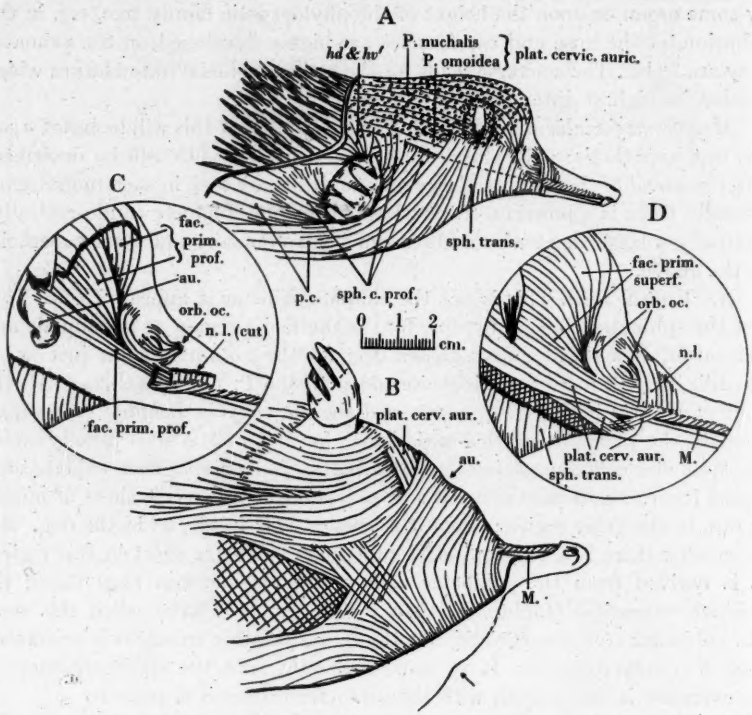


Fig. 2. *Echidna aculeata*. Z.P.2. × ½.

its true nature. The muscle—misnamed by Schulman the M. hyomandibularis —takes origin from the hyoid region and from the mid-ventral plane rostral to this. Its fibres run obliquely rostro-dorsally to gain attachment to the whole of the serrated, soft portion of the lower bill.[2] This serrated area lies lateral to the mandible and extends from the angle of the mouth almost to

[1] The superficial caudal fibres (Fig. 2A) form a very thin sheet which covers and conceals the more powerful and numerous fibres that pass deep to the platysmo-cervico-auricularis (Fig. 2 A, B).

[2] The muscle is called by Meckel the M. cutaneus labii inferioris; he describes it as risorio comparandus!

the rostral end of the bill. It constitutes a lower lip which functions during the suctorial feeding.[1]

B. *Dorsal sheet.* This takes origin from the mid-dorsal line—caudal to the skull—and from the shoulder region; its fibres are inserted into the auricular cartilage and into the facial region. To gain this the fibres in *Ornithorhynchus* pass wholly ventral, those of *Echidna* pass dorsal and ventral, to the external auditory opening. This sheet is probably a composite one. The fibres which take origin from the shoulder region in *Echidna*, and from the arm—near the elbow—in *Ornithorhynchus* are homologous with the omoideal fibres of the notoplatysma[2] (*csd1c*; Figs. 2A, 4A, B). But the fibres which take origin from the mid-cervical line and are inserted into the auricular cartilage (in both genera), and the fibres which, in *Echidna*, stream across the vertex to gain the facial region, are homologous with the M. cervico-auriculo-occipitalis[3] (*csd2a*). The intermediate fibres (present mainly in *Ornithorhynchus*; they pass ventral to the ear to gain the facial region) represent the nuchal fibres of the notoplatysma (*csd1c*) accompanied by fibres from the M. cervico-auriculo-occipitalis (*csd2a*; cf. Fig. 1B, C). The whole sheet, therefore, is taken to be a fusion of these two muscles and to be a platysmo-cervico-auricular complex.

The insertion of the platysmo-cervico-auricularis is as follows: In *Ornithorhynchus* the ventral (omoideal) fibres remain entire; they cover the cheek pouch and its musculature and end in the gular region. The remainder of the fibres splits into two layers, ventral to the orbit. The delicate, thin, superficial sheet ends at the bases of the dorsal and ventral integumentary flaps; the deeper fibres are attached to the maxilla deep to the dorsal integumentary flap. In *Echidna* the ventral fibres remain entire; they pass ventral to the ear and are inserted into the maxilla close to the M. naso-labialis. The remainder of the fibres stream across the vertex dorsal to the ear. In the facial region they split into four incompletely separated layers—a superficial sheet and three deeper derivatives (Fig. 2, insets C, D).[4] They gain attachment to

[1] When feeding on mud and worms the animal behaves as an animated vacuum cleaner. Burrell—who aptly calls this soft portion of the bill the 'lip'—suggests that a 'small central suction tube' is formed. The anatomical findings suggest that the sphincter colli profundus depresses the lower lip and allows food to be sucked in laterally towards the anterior tongue.

[2] The facialis musculature of monotremes bridges the gap between that of the reptile and of the marsupials and placentals. It has been homologized here with the fully developed musculature of these vertebrates but reference has already been made to the primitive matrices.

[3] In selachians, amphibians and reptiles the *csd2a* and *L2* musculatures are closely associated—they may be inseparable—and form the *cL2* musculature. In monotremes the same condition may apply; but in these there is no attachment of fibres to the skull, and so the *L2* fibres are not recognizable. They seem not only to have fused with the overlying *csd2a* fibres but, through them, to have gained a secondary attachment to the ligamentum nuchae. This may have been caused by the massive attachments to the posterior half of the skull—dome as well as base—of the powerful muscles of the neck. In the absence of less highly specialized monotremes, the above assumption seems necessary to account for the well-developed derivates of the *L2* musculature present in higher mammals.

[4] The only portion of the musculature to attain any degree of independence is the most ventral of the deeper sheets (M. auriculo-maxillaris, Ruge). The remainder are fused with the superficial sheet and gain their short independence close to their insertions (Fig. 2C).

the whole of the zygomatic arch and to the maxilla rostral to this. These muscle layers represent the first or primitive stage in the formation of a facial musculature.

Subjacent to the platysmo-cervico-auricularis in the dorsal cervical region is found a third well-developed muscle sheet (Fig. 4C, D). This takes origin from the mid-dorsal line of the neck and from the occipital region—where it lies superficial to the attachments to the skull of powerful nuchal muscles; it has no attachment to the skull. The direction of its fibres is ventro-caudal; in *Echidna* they reach the forearm,[1] in *Ornithorhynchus* they may or may not reach the arm (Fig. 4C, D). This sheet (M. cranio-humeralis of Ruge) is homologous with the M. cervicalis transversus. In monotremes neither this muscle nor the sphincter transitus gives rise to other muscles.

In certain regions of the face, however, distinct and discrete muscles have been dissociated from their matrix. In *Echidna* there are Mm. buccinator, orbicularis oculi—whose ventral fibres are better developed than the dorsal—and naso-labialis. In *Ornithorhynchus* the M. orbicularis oculi is better developed dorsally[2] than ventrally; there is a well-marked M. buccinator, a cheek-pouch musculature and a M. mentalis (these are not shown in the diagrams);[3] a more or less complete ring of muscle in the bases of the integumentary flaps; also some muscles in the ear-eye region which are almost completely independent. Though the projection of the auricular cartilage is much less in *Ornithorhynchus* than in *Echidna*, the muscles in connexion with that have attained a greater degree of independence; they exhibit minor variations. In neither monotreme is there a M. digastricus posterior, but in each there is a M. stylohyoideus; this is powerful in *Echidna*, but feeble in *Ornithorhynchus* (Figs. 3A, 4E).

Though not part of the facialis musculature the Mm. digastricus anterior and mylohyoideus of monotremes deserve mention (Figs. 3A, 4E). The M. mylohyoideus of mammals is homologous with the P. intermandibularis of elasmobranchs which is attached to the medial surface and ventral margin of Meckel's cartilage. When the dentary bone encloses this the M. mylohyoideus becomes attached to the bone *at the level of Meckel's cartilage*. This attachment is usually to the medial surface of the bone; but, under certain conditions, the dentary bone appears to split the mylohyoid matrix into two layers; the one gains attachment to the medial, the other to the lateral surface of the bone. Both these layers are present in the monotremes[4] and have been called the Mm. mylohyoideus superficialis and profundus. In both muscles the direction of the rostral fibres differs from that of the caudal, though both

[1] Neither Ruge nor Huber describe this muscle in *Echidna*; Westling's description is indefinite.

[2] Part of this may represent a M. naso-labialis.

[3] The M. mentalis is well developed. It compresses the anterior portion of the lower 'lip' against the upper.

[4] A two-layered M. mylohyoideus is present in certain mammals, e.g. sheep (Bertelli, 1927).

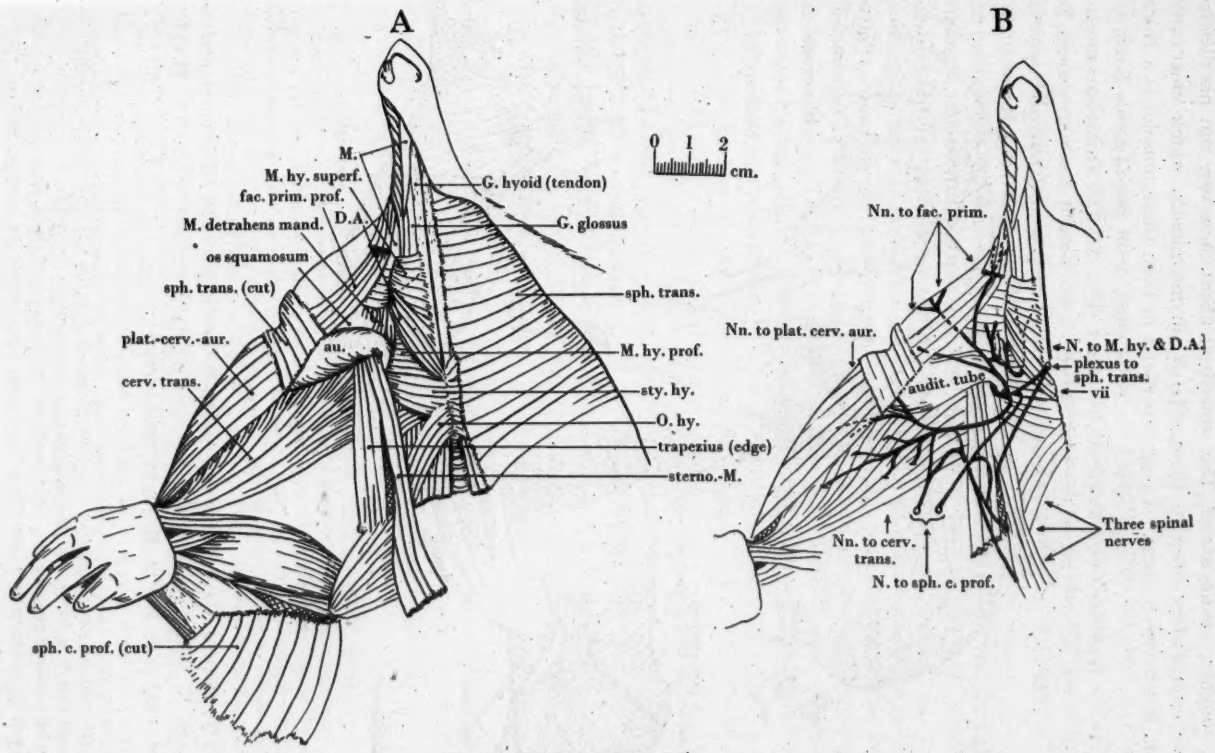


Fig. 3. *Echidna aculeata*. Z.P.2. × 1.

are, roughly, medio-lateral. The superficial fibres, however, run parallel to those immediately deep to them. The N. mylohyoideus, which innervates both, lies between them.[1] Lying superficial to both these muscles is a third

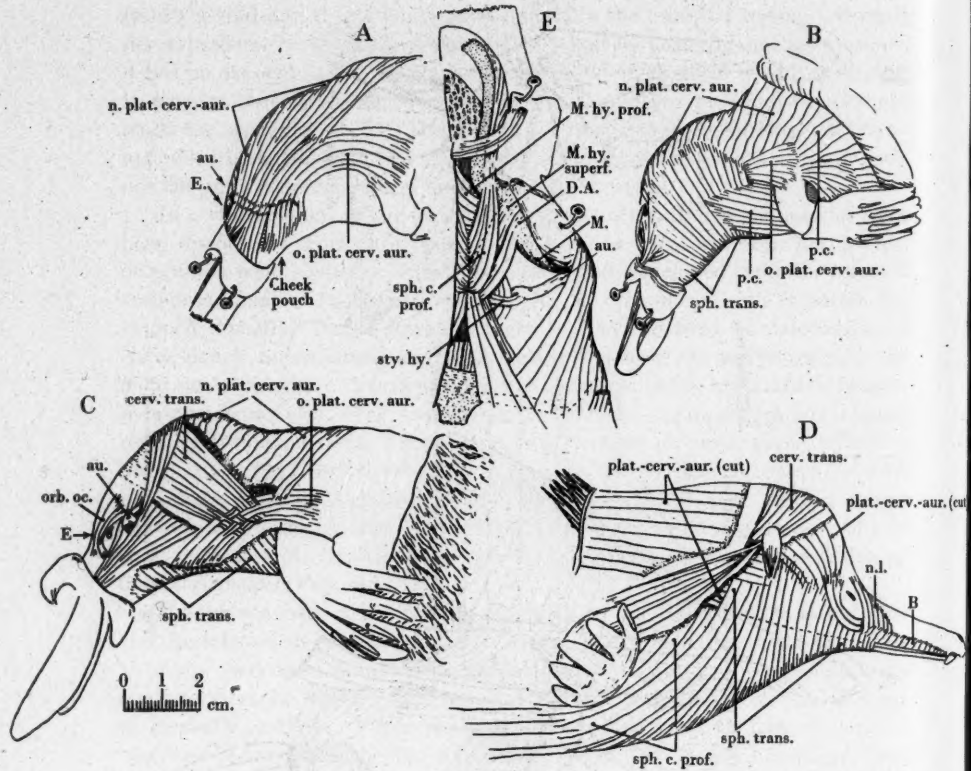


Fig. 4.

discrete muscle whose fibres run obliquely medio-laterally. This is innervated by the N. mylohyoideus which enters its deep surface (Figs. 3A, B, 4E). This is taken to be the M. digastricus anterior.

[1] The unusual position of the N. mylohyoideus—deep to the M. mylohyoideus superficialis—suggests that this muscle and the M. digastricus anterior are derived from a common matrix. In which case both muscles, or neither, would be the derivative of the M. mylohyoideus according to the truth or otherwise of the above hypothesis. The evidence, at present available, suggests that it is probably correct.

## SUMMARY

Brief descriptions have been given of three hypotheses, and a longer account of a fourth, more recent, and little-known hypothesis, of the origin of the mammalian facialis musculature. According to this the dorsal post-auricular facialis musculature of sub-Mammalia gives rise to the major portion of the facial musculature in Mammalia.

Such conditions are fulfilled, almost diagrammatically, in the dorsal musculature of monotremes. Ventrally, their sphincter sheet has been homologized with the sphincter transitus of marsupials and rodents.

A sphincter colli profundus is present but differs in each genus; in *Echidna* it is mammalian, in *Ornithorhynchus* more reptilian in character. The intermandibular musculature—which lies deep to the sphincters colli profundus and transitus and is innervated by the Vth—has three layers, apparently representing the Mm. digastricus anterior, mylohyoideus superficialis and mylohyoideus profundus.


In conclusion I wish to thank Prof. Burkitt for his continued interest and assistance in this work; and the Department of Anatomy, University of Sydney, for the supply of material and the granting of facilities for conducting this investigation.

## ABBREVIATIONS

*au.* = auricular tube or opening; *au.p.* = M. auricularis posterior; *B.* = M. buccinator; *cerv.-aur.-occ.* = M. cervico-auriculo-occipitalis; its two components are *cerv.-aur.* = M. cervico-auricularis and *cerv.-occ.* = M. cervico-occipitalis; *cerv.trans.* = M. cervicalis transversus, called by Ruge M. cranio-humeralis; *D.A.* and *D.P.* = Mm. digastricus anterior and posterior; *E.* = eye; *fac. prim.superf.* and *fac.prim.prof.* = superficial and deep primitive facial muscles which are continuous with, or only partially separated from, their matrix. Ruge names these the Mm. maxillo-nuchalis, maxillaris profundus, maxillo-auricularis superior and inferior. The last seems analogous to the M. auriculo-labialis. *M.* = mandible; *M.A.* = M. mandibulo-auricularis; *M.hy.superf.* and *prof.* = M. mylohyoideus superficialis and profundus; *N.* and *Nn.* = nerves; *n.-l.* = M. naso-labialis, *n.-plat.* = noto-platysma; *n.n.-plat.* = nuchal fibres of noto-platysma; *n.plat.-cerv. aur.* = nuchal fibres of M. platysmo-cervico-auricularis, called by Ruge the M. maxillo-nuchalis; *o.n. plat.* = omoideal fibres of noto-platysma; *o.plat.-cerv.-aur.* = omoideal fibres of the platysmo-cervico-auricularis, called by Ruge the M. maxillo-humeralis; *occ.* = M. occipitalis; *occ.-pol.* = M. occipito-pollacalis; *orb.oc.* = M. orbicularis oculi; *p.c.* = panniculus carnosus; *P.orb.*, *P.jug.*, *P.alv.*, *P.prof.* = pars orbitalis, jugalis, alveolaris and profunda of the M. maxillo-naso-labialis; *plat.-cerv.-aur.* = M. platysmo-cervico-auricularis; *sph.c.prof.* = sphincter colli profundus; *sph.t.* = sphincter transitus; *sty.hy.* = M. stylohyoideus.

## LIST OF DIAGRAMS AND THEIR LEGENDS

All diagrams with scale attached are dioptograms

Fig. 1. Schema of dissections; A, of hypothesized reptile; B–D, of hypothesized primitive mammal; E–F, of extant mammals. Details of the dorsal musculature are shown in all diagrams, but portions of the ventral musculature are shown in A and B only. A. Reptilian head showing the superficial sheets *csd1c* (P. noto-gnathica) and *csv1c* (P. mandibularis); also the deeper ones *cL2* (P. cephalo-gnathica) and *csv2a* (P. interhyoidea). The P. cephalo-gnathica consists of two portions, the P. epiphyoidea (*csd2a*) and the second levator (*L2*); these may be partially or completely fused. The P. interhyoidea is homologous with the M. stylohyoideus of higher forms, but is only shown in this diagram. B. Primitive mammal, superficial dissection. Note that the P. noto-gnathica becomes the noto-platysma and the P. mandibularis the sphincter colli profundus. The omoideal fibres of the noto-platysma were, probably, not present in primitive mammals but are shown here to save a diagram. C. Dissection of primitive mammal, after removal of the noto-platysma and the sphincter colli profundus, to display the superficial expansion of the P. cephalo-gnathica (*cL2*). The sheet passes dorsal as well as ventral to the external opening of the ear and covers the whole of the facial area. No individual muscles are seen. D. Deep dissection of a primitive mammalian head to display the splitting of the P. cephalo-gnathica into superficial and deep layers. The high degree of subdivision shown in the pre-orbital region is not a primitive one but is shown here to save a diagram. In the post-auricular region the deep derivatives of the P. cephalo-gnathica are inseparable from and concealed by the superficial sheet, but their subsequent development is shown in E and F. E. Superficial dissection of the post-auricular region in extant mammals to show the derivatives of the P. epihyoidea (*csd2a*) which have retained their original attachment to the mid-nuchal line. They are the Mm. cervico-occipitalis, cervico-auricularis and cervicalis transversus. F. Deep dissection of the post-auricular region in extant mammals to show the derivatives of the second levator (*L2*) which have retained their original attachment to the skull. They are the Mm. mandibulo-auricularis (a variant), digastricus posterior, occipitalis, auricularis posterior and the occipito-pollacalis of bats.

Fig. 2. A. *Echidna* $\times\frac{1}{2}$; lateral view to show the distribution of the platysmo-cervico-auricularis and the sphincteres colli profundus and transitus. B. *Echidna* $\times\frac{1}{2}$; ventral view to show the two sphincters and their relation to the panniculus carnosus. C. *Echidna* $\times 1$; inset to show the three portions of the deep primitive facial muscles and their incomplete separation from the platysmo-cervico-auricularis matrix. The most ventral has gained the greatest independence. The dissociation from the matrix has been exaggerated in the diagram. D. *Echidna* $\times 1$; inset to show the superficial primitive facial musculature continuous with its matrix.

Fig. 3. *Echidna* $\times 1$; ventral view. A. Deep dissection to show the Mm. cervicalis transversus, stylohyoideus, digastricus anterior, mylohyoideus superficialis and profundus and the two heads of the detrahens mandibulae. Note the caudal end of the mandible lying dorsal to this muscle. B. Deep dissection to display the Nn. facialis (vii) and mylohyoideus.

Fig. 4. A. *Ornithorhynchus* $\times\frac{1}{2}$; oblique lateral view. The sphincter transitus has been removed to display the nuchal and omoideal fibres of the platysmo-cervico-auricularis. B. *Ornithorhynchus* $\times\frac{1}{2}$; oblique lateral view. This shows the relationships of the sphincter transitus to the platysmo-cervico-auricularis and the panniculus carnosus. C. *Ornithorhynchus* $\times 1$; lateral view. Deeper dissection to show the M. cervicalis transversus. The sphincter transitus and the platysmo-cervico-auricularis have been partially removed. D. *Echidna* $\times\frac{1}{10}$; lateral view to display the M. cervicalis transversus as in the preceding diagram. E. *Ornithorhynchus* $\times 1$; ventral view to display the sphincter colli profundus (innervated by vii), Mm. digastricus anterior, mylohyoideus superficialis and profundus and stylohyoideus.

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[1] Not available.

# THE TETRAPOD KNEE JOINT

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Advance in knowledge of the comparative anatomy of joints has generally lagged behind that of other structural systems. Bland Sutton (1884, etc.) has discussed the possible origin of various ligaments; the classical descriptions of the British school of myologists (Owen, Wood, Macalister, Windle, etc.) contain some reference to arthrology; and Parsons (1900, etc.), in his work on mammalian joints, has assembled a large amount of arthrological information, representing a fairly adequate survey of the Mammalia as a whole, and forming a substantial basis for all subsequent research. Primates have been studied in some detail (Keith, 1894; Westrienen, 1907; Sonntag, 1924), but even for mammals, apart from the larger domesticated forms, full descriptions and illustrations of the articular surfaces and associated ligaments are rare, whilst the detailed mechanism of reptilian joints is almost unknown.

The knee joint has here been chosen for special study, as representing a large and functionally important articular unit, provided with an extensive synovial cavity and a variety of both intra- and extra-articular structures, and frequently associated with such additional ossifications as the patella, lunulae and fabellae. These various structures have often attracted attention, and the suggestions that have been made concerning their origin and history are discussed in the text. Further, as suggested by Taylor & Bonney (1905) in their work on the popliteus, the knee joint is of peculiar interest as manifesting a change of mechanism in passing from reptiles to mammals, and as affording a means of studying the corresponding modifications of anatomical structure.

There are described in this paper examples of knee joints from every extant order of Reptilia and Amphibia with limbs, as well as examples from prototherian, metatherian and eutherian mammals. This material has been obtained partly from the Physiological Store Collections of the Royal College of Surgeons Museum through the kindness of Prof. Cave, and partly from purchases made by a grant from the Thomas Smythe Hughes Fund.

The following species have been personally studied by dissection:

*Necturus maculatus*
*Salamandra maculosa*
*Megalobatrachus japonicus*
*Rana catesbiana*
*Xenopus laevis*
*Bufo vulgaris*
*Crocodilus porosus*
*C. niloticus*
*Emys blandingii*
*Sphenodon punctatum*

*Varanus varius*
*V. niloticus*
*V. exanthematicus*
*Iguana tuberculata*
*Tupinambis teguexin*
*Gallus domesticus*
*Ornithorhynchus paradoxus*
*Echidna* sp.
*Didelphys virginiana*
*D. philander*
*D. marsupialis*
*Macropus rufus*
*Sciurus caroliensis*
*Felis domesticus*

### *CROCODILUS POROSUS*

There are but two extant groups of reptiles the structure of whose bones, particularly in the epiphysial region, still resembles that in the early tetrapods; they are the chelonians and crocodiles (Haines, 1938). Of these the chelonians show a highly specialized knee joint described later, leaving the crocodiles as the most important living group illustrating primitive conditions before the phylogenetic development of the patella or of large epiphysial cartilages with secondary centres.

#### *Crocodilus*

The femur presents two condyles, the lateral larger than the medial, and a concave facet for the head of the fibula. The tibia presents two slightly convex surfaces which meet at an angle, but no very distinct intercondylar eminence. The fibula is separated by a small gap from the tibia, but bears a facet for articulation with the femur.

The single synovial cavity of the knee joint includes both condyles and the femoro-fibular joint, there being no trace of subdivision of the cavity. The origin of the long crural extensor muscle lies entirely outside the joint cavity. The tibial and fibular collateral ligaments both show twisting of their fibres, the outer fibres of the fibular ligament running forwards and those of the tibial ligament backwards as they pass from the femur. The tibio-fibular ligament is relatively slender. The joint cavity enclosed by the capsule extends over all three bones as far as the edge of the cartilage, but does not encroach on the bony shaft.

The two menisci are both massive structures fitted between the highly incongruent opposed surfaces of femur and tibia. Anteriorly they are connected by an intermeniscal ligament and are attached to the femur and to the tibia by menisco-femoral and menisco-tibial ligaments respectively. Posteriorly both menisci are attached to the femur by the posterior menisco-femoral ligaments, that from the lateral meniscus passing posterior to the other. All these ligaments, as well as the peripheral margins of the menisci, are attached to the inner surface of the capsule. The cruciate ligaments (the two anterior embracing the single posterior ligament) are each separately and completely surrounded by the joint cavity, and so are intrasynovial structures in the same sense as is the tendon of the long head of the biceps in man. The

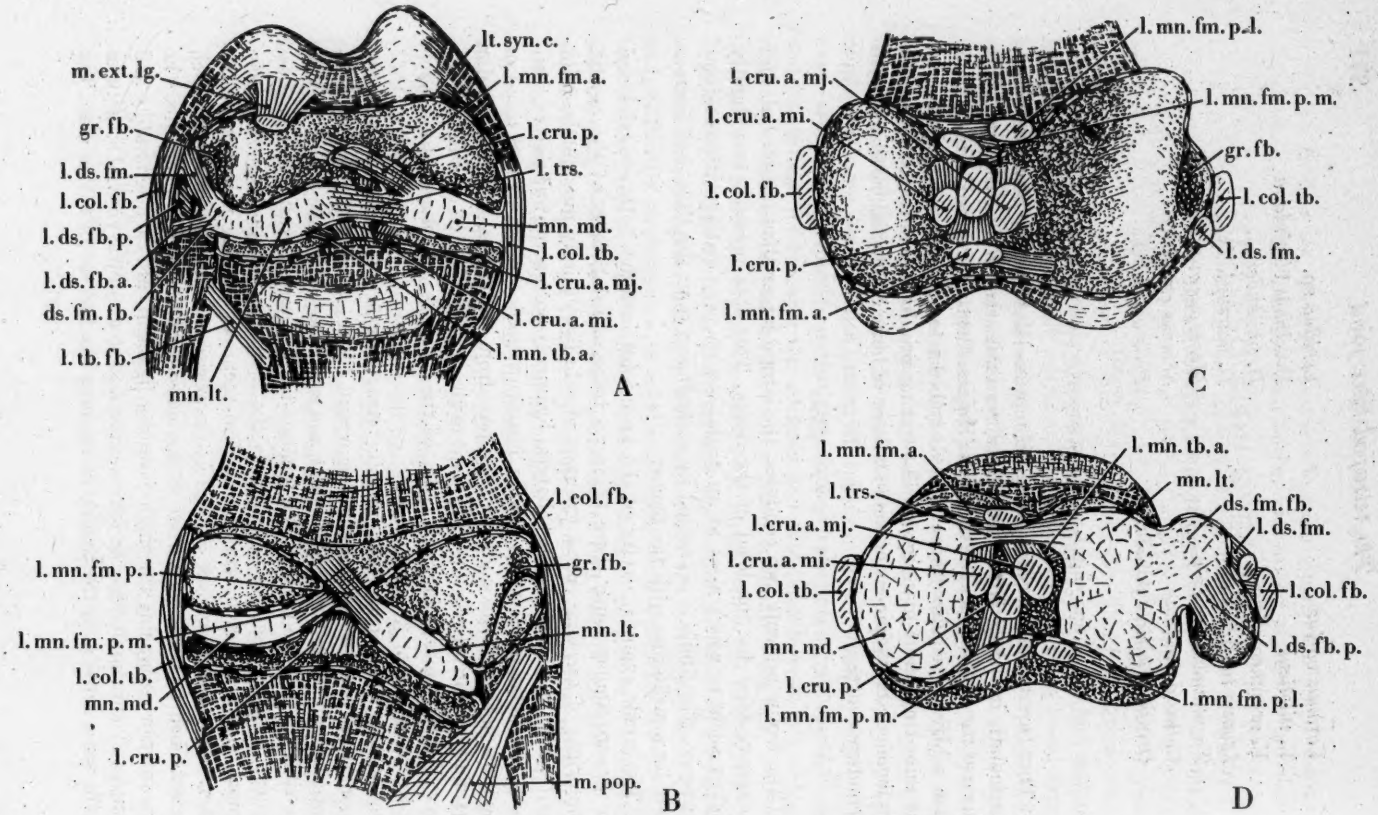


Fig. 1. Knee of *Crocodilus porosus*. A, anterior view, flexed. B, posterior view, extended. C, articular surface of femur. D, articular surfaces of tibia and fibula, with menisci and femoro-fibular disc.

cruciate ligaments occupy most of the space between the two menisci, thus rendering extremely narrow the actual passage between the synovial spaces above and below.

Whether there is actually a synovial membrane covering the cruciate ligaments is uncertain. In mammals a distinct cellular layer can be found covering loose connective tissue and fat, but in the regions where dense connective tissue, tendons and ligaments come into close relationship with the joint cavity no clear distinction can be made between the tissues of the joint surface and the underlying structures, and a reclassification of synovial structures based on the substratum on which they lie has been suggested (Key, 1932). In reptiles the structure of the synovial surfaces resembles that in mammals, but there is less fat within the joint capsule (Lubosch, 1910). In view of these difficulties the term synovial membrane is avoided in the description of the gross structure of joints, and the extent of the joint cavity is described rather than the position of reflexions of the synovial membrane. It is this extent that is indicated by broken lines in the figures, and when structures, such as the cruciate ligaments, are shown lying within the limits of the joint cavity, it is implied that they are intra-synovial in position.

Continuous with the lateral meniscus is the femoro-fibular disc, a fibrocartilaginous pad occupying the anterior part of the femoro-fibular joint. It is attached to the femur by a disco-femoral ligament and to the fibula by anterior and posterior disco-fibular ligaments. The posterior disco-fibular ligament is attached over the whole width of the fibular head so that the cavity of the joint between the disc and the fibula is continuous with that between disc and femur only by way of the central opening between the menisci.

*Movements.* Flexion and extension take place between the femur and the underlying structures. In all positions the cruciate ligaments are sufficiently taut to prevent direct antero-posterior gliding between the tibia and femur, so that the movement is controlled throughout by these ligaments which rigidly determine the relative positions of the two bones as in mammals (Haines, 1941). As the joint is extended the femur rolls forward on the tibia to a slight degree carrying the menisci with it. This movement resembles that in man, described by Fick (1910). At the same time the pull of the femur through the posterior menisco-femoral ligaments approximates the posterior parts of the menisci. Rotation of the tibia on the femur occurs round an axis determined by the crossing of the cruciate ligaments midway between the menisci, so that as the one condyle moves forwards on the tibia the other moves backwards, the condyle and the corresponding meniscus moving together on the tibia. Each articular surface on the head of the tibia is larger than the corresponding meniscus, thus permitting movement of the meniscus during rotation. The antero-posterior excursion of the fibula is limited by the groove in which it lies and in which it is firmly held by the disco-fibular ligament. Thus as the femur rotates the fibula follows that bone, and not the tibia. The detailed mechanism of rotation will, however, be discussed later.

surfaces of tibia and fibula, with menisci and femoro-fibular disc.

According to Fürst (1903) and Nauck (1938), the menisci of *Alligator* are less extensive and only two cruciate ligaments are figured, but the arrangement is similar to that in the crocodile.

### *SPHENODON PUNCTATUM*

The single joint cavity has a large expansion behind the quadriceps tendon, and posteriorly there are small extensions of the cavity above the femoral condyles, but otherwise the limits of the cavity follow closely those of the articular cartilage. The origin of the long crural extensor and the insertion of the common tendon of the flexores intercapitales both lie outside the joint cavity though both indent it. The popliteus arises from the fibula and has no relation to the joint cavity.

The fibular collateral ligament shows crossing of its fibres, a condition not detected, however, in the tibial collateral ligament. The anterior tibio-fibular ligament lies immediately below the knee joint. Anteriorly, the medial meniscus is attached to the femur by the anterior menisco-femoral ligament and to the tibia by a slender ligament which joins the tibial collateral, and the lateral meniscus is attached to the tibia by a large anterior menisco-tibial ligament. Posteriorly, both menisci are attached to the femur between its condyles, the attachments crossing each other, and the lateral meniscus is further attached by means of a posterior menisco-tibial ligament. The menisci themselves are both C-shaped, with well-marked indentations, and neither is as heavily built as the crocodilian meniscus. A small extension of the joint cavity passes between the medial meniscus and the tibial collateral ligament. The lateral meniscus contains anteriorly a small bone, the lunula (here described, it is believed, for the first time in *Sphenodon*). The anterior cruciate ligament is double, with a thinner medial and a thicker lateral portion, and between them is the posterior cruciate ligament. The femoro-fibular disc is small and is attached by ligaments to the lateral meniscus, the femur and the fibula.

The movements possible at the knee joint are similar to those described for the crocodile (q.v.).

The smallness of the animal and the difficulty of obtaining material may render the description of *Sphenodon* a little less accurate than that of the other types discussed. Further, its isolated zoological position precludes confirmation of the description submitted by any comparison with closely related types.

### *VARANUS VARIUS*

The femur has the usual reptilian form, presenting two condyles and a concave facet for articulation with the fibula, and also a deep groove for the patella which, as in other lizards, is ossified. The tibia and fibula lie close together, but do not actually articulate. The single joint cavity extends over

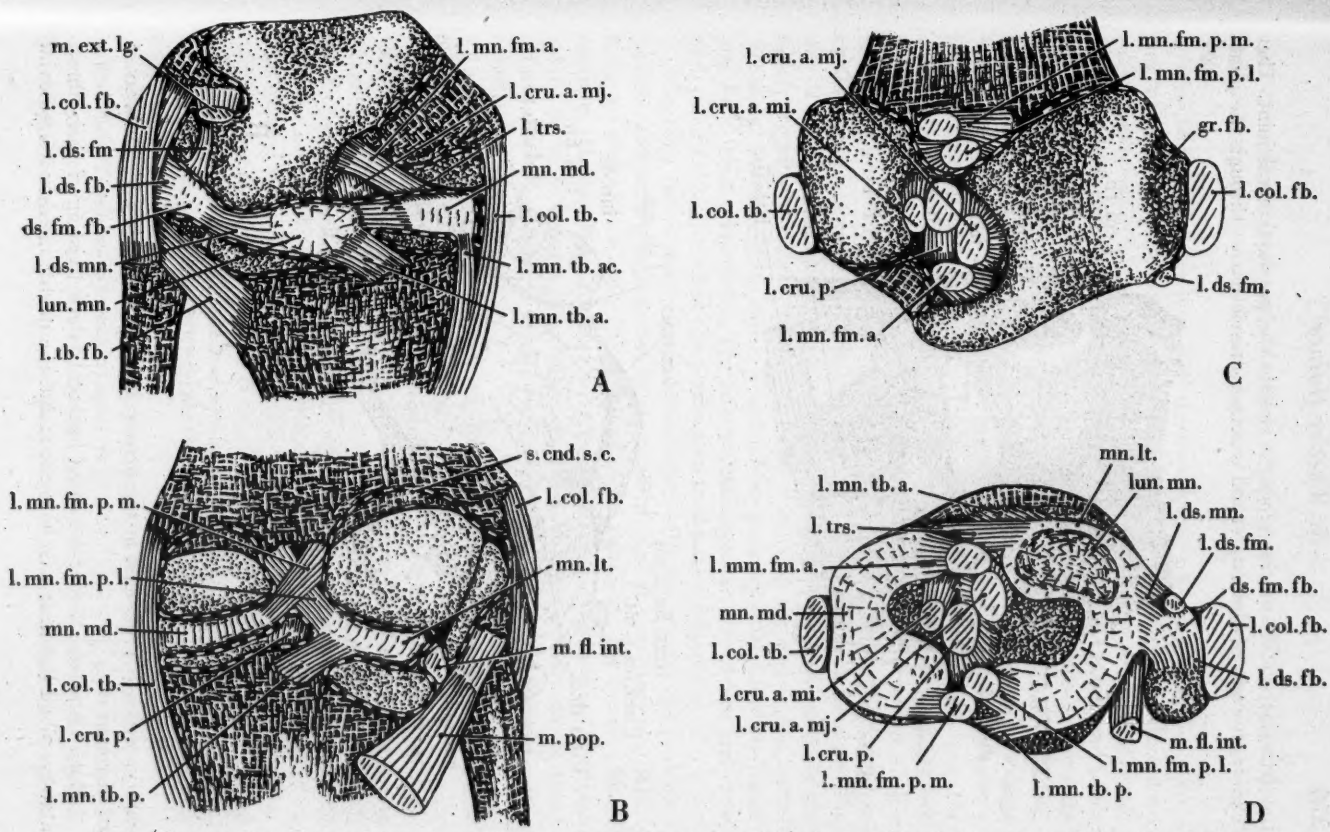


Fig. 2. Knee of *Sphenodon punctatum*. A, anterior view, flexed. B, posterior view, extended. C, articular surface of femur. D, articular surfaces of tibia and fibula, with menisci and femoro-fibular disc.

the articular surface of the femur to include the patello-femoral joint. The tendon of origin of the long crural extensor muscle passes through the joint

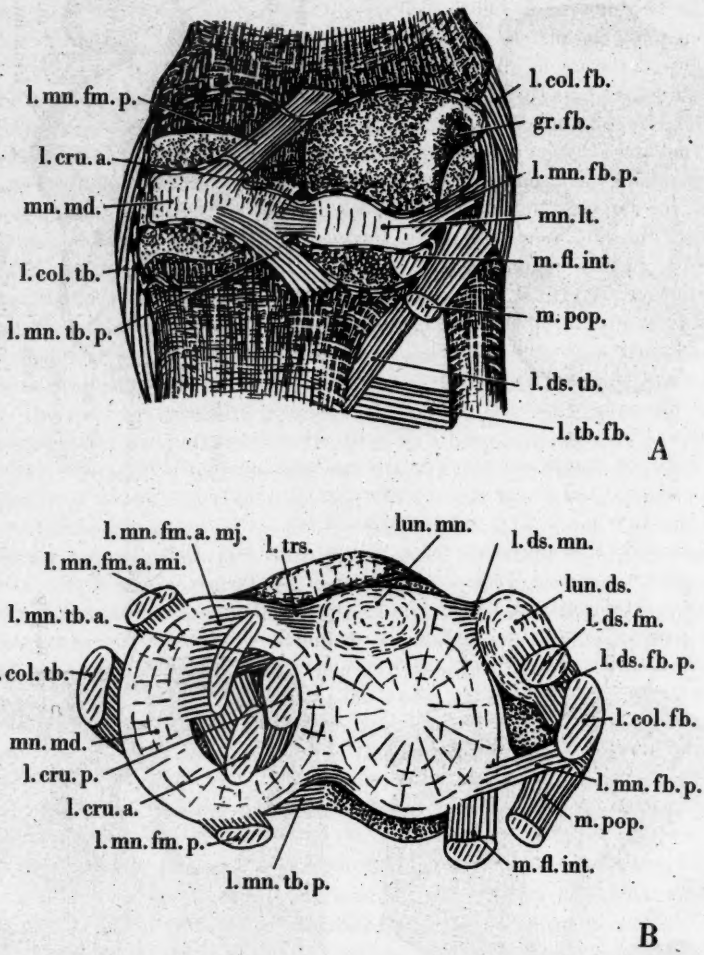


Fig. 3. Knee of *Varanus varius*. A, lateral view, semi-flexed. B, articular surfaces of tibia and fibula, with menisci and femoro-fibular disc.

cavity, which is prolonged in the groove between the tibia and fibula so as to surround it.

Both tibial and fibular collateral ligaments show twisting of their fibres, and the tibial ligament has, between it and the medial meniscus, a synovial

cavity opening at each end into the main joint cavity. The anterior tibio-fibular ligament is a strong band placed at some distance from the knee joint.

The two menisci are both well developed, but while the lateral is a continuous mass completely separating the femoral and tibial joint cavities from each other, the medial is a circular structure with a perforation in its centre through which pass the cruciate ligaments. Thus the cavities above and below the menisci communicate in three places: (1) through a passage between the tibial collateral ligament and the medial meniscus, (2) through the perforation in the medial meniscus, and (3) on the lateral side of the lateral meniscus below the femoro-fibular joint. The medial meniscus is attached anteriorly by two anterior menisco-femoral ligaments, the larger attached near the anterior cruciate ligament, the other near the tibial collateral, and by two anterior menisco-tibial ligaments. The lateral meniscus is attached to the fibula by a posterior menisco-fibular ligament, but is otherwise held in position by its connexion with the medial meniscus and the femoro-fibular disc. The disc is attached antero-inferiorly by disco-tibial and disco-fibular ligaments which are attached partly to the ligament connecting the disc to the lateral meniscus. Posteriorly the disc is held firmly in place by posterior disco-fibular and disco-femoral ligaments. The two cruciate ligaments are strong and cross each other as they traverse the perforation in the medial meniscus.

The tibia has a facet for an articulation with the quadriceps (patellar) tendon as that structure passes to its insertion, and the cartilage also forms a lip for articulation with the tibial collateral ligament. The flexores intercapitales (Haines, 1934) form a strong common tendon which enters the joint cavity so as to become completely intra-articular on its way to its tibial attachment. The popliteus takes origin from the fibula and is entirely extra-articular.

In the antero-medial part of the lateral meniscus is an ossified lunula, and the interior of the disc is also bony.

*Movements.* Flexion and extension are very free, the former being associated with some forward gliding of the menisci on the tibia. The cruciate ligaments have, in comparison with those of other reptiles examined, a more medial position, so that rotation at the knee takes place around an axis passing near the centre of the medial condyle, and not between the two condyles. The menisci move with the femur, the lateral meniscus performing a considerable excursion on the lateral condyle of the tibia which accordingly bears a large articular facet. The fibula also shows the usual reptilian arrangement, moving with the femur in the socket formed for it by the grooved facet on the femur and the disc.

Other lizards examined (*Iguana tuberculata*, *Ctenosaurus* sp., *Conolophus subcristatus*, *Tupinambis teguexin*) agree well with *Varanus* in general arrangement, except in the number of lunulae—usually three, as in all the animals listed, but sometimes four as in *Varanus niloticus*, *Trachysaurus rugosus*,

*Corucia zebrata* (Pearson & Davin, 1921). They always occupy the same morphological position, the interior of the thicker parts of the semilunar cartilages.

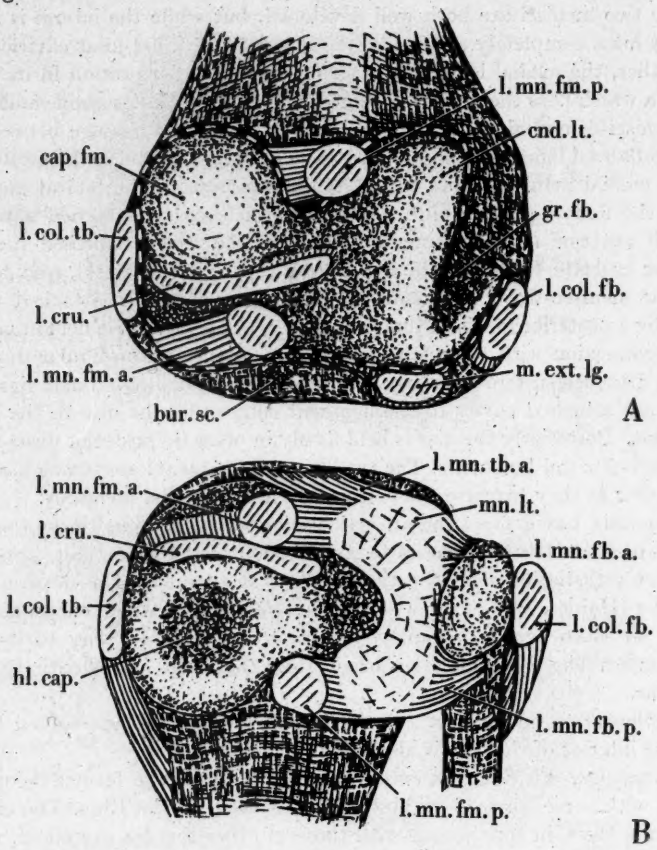


Fig. 4. Knee of *Emys blandingii*. A, articular surface of femur. B, articular surfaces of tibia and fibula, with meniscus.

### *EMYS BLANDINGII*

In *Emys blandingii*, as in other chelonians, a patella is wanting, but a separate subcrureal bursa occurs, completely separated from the synovial cavity of the knee joint proper by a thin fibrous septum. The origin of the long crural extensor muscle lies outside both cavities. The main cavity presents a posterior recess above the lateral condyle.

The medial condyle of the femur has been reduced to a more or less hemispherical capitulum resembling that at the lower end of the human humerus.

This capitulum articulates directly with a fossa on the tibia, there being no meniscus in the medial part of the joint. The lateral condyle has the usual form, and a well-developed meniscus is present in the lateral part of the knee joint. Laterally, the femur presents a well-developed facet for the fibula, and the articular cartilage is continued to the femoral attachment of the fibular collateral ligament to form a small facet over which this ligament can glide.

The collateral and tibio-fibular ligaments are arranged as in other reptiles examined, the fibular collateral manifesting the usual crossing of its deeper by its more superficial fibres. The meniscus is C-shaped and is attached to the bones by five ligaments—to the femur by an anterior and a posterior menisco-femoral ligament, to the fibula very closely by an anterior and a posterior menisco-fibular ligament, and to the tuberosity of the tibia by a menisco-tibial ligament. A single flat intrasynovial cruciate ligament passes from tibia to femur anterior to the joint between the capitulum and its socket.

Movement of the knee joint is limited to some flexion and extension and to some rotation, but no movement is as free as in the case of the other reptiles described. The capitulum is firmly held in its socket so that there is no rolling of the femur on the tibia. Rotation of the tibia occurs about the centre of the capitulum as an axis, so that, for a given amount of rotation, the lateral condyle has further to move than when the axis passes between the two condyles. The meniscus and fibula are firmly bound together by the menisco-fibular ligaments, and the fibula is closely locked to the lateral condyle of the femur, so that during rotation the fibula moves with the femur rather than with the tibia.

Clearly this is a very specialized joint. The apposition of the capitulum to its socket offers great resistance to dislocation, but movement is limited as the bony surfaces at the margins of the capitulum and socket soon come into contact, particularly when the joint is extended. The extreme mobility of the chelonian hip joint and the peculiarities of the chelonian gait render a high range of knee joint extension unnecessary. The loss of the medial meniscus follows the change in the type of joint. The lateral meniscus preserves the old attachments to the femur and also develops a new ligament to the tibia. The loss of the femoro-fibular disc may also be correlated with the limitation of movement.

Other chelonians appear to be similar. Bojanus (1821) shows in *Testudo graeca* the collateral, menisco-tibial, cruciate ('lig. cruciatum internum') and posterior menisco-femoral ('lig. cruciatum externum'), and notes a small anterior lunula which I have not found in my specimens. The medial meniscus may appear as a narrow rim of tissue (Fürst, 1903, *Emys lutaria*), but is never a well-developed structure as in crocodilians.

### AMPHIBIA

As noted by Bland-Sutton (1884, etc.) the tailed Amphibia present the simplest known form of knee joint. In the largest form, *Megalobatrachus*, the femur bears two poorly developed condyles separated anteriorly by a groove for the origin of the crural extensor muscle mass. The tibia and fibula articulate firmly with each other. A fibrous sheath surrounds the whole knee joint and is prolonged downwards around the superior tibio-fibular joint. Outside the sheath are two relatively short collateral ligaments. No joint cavity exists within the sheath, the whole of the space between the two bones (femur, tibia) being filled with a pliant fibro-vesicular tissue, whose detailed structure has been carefully studied by Lubosch (1910).

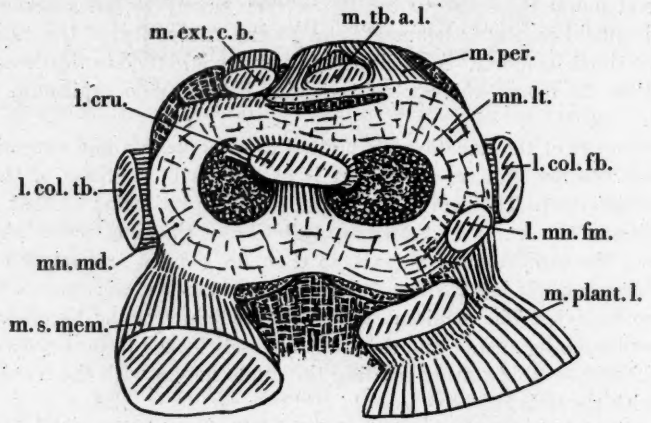


Fig. 5. Knee of *Rana catesbiana*, articular surface of tibio-fibula, with menisci.

In some urodeles a true cavity is present in the knee joint. In *Salamandra maculosa*, for instance, this cavity extends between the femur and the fibula and also over the more lateral part of the upper surface of the tibia, but the more medial part of the joint is filled by fibro-vesicular tissue. Lubosch considered this mass of tissue as constituting a meniscus, but though it may be derived phylogenetically from a meniscus it bears no anatomical resemblance to such a structure in *Salamandra*. Indeed, if, as suggested later, the knee joints of modern urodeles are derived—by a process of phylogenetic simplification—from more complex primitive forms, the fibro-vesicular tissue would be derived not only from the menisci but also from the other ancestral intracapsular structures, particularly the cruciate ligaments.

Other urodeles studied agree in structure with those discussed, and in all forms examined flexion is free whilst rotation is very limited.

Gaupp (1896) has given a good, though unillustrated, account of the knee joint in the anuran *Rana*, which is here amplified in certain particulars from my own dissections of *Rana catesbiana*.

Anteriorly three muscles arise from the femur—Gaupp's m. extensor cruris brevis, m. tibialis anticus longus and m. peroneus, corresponding to the crural extensor and peroneal musculature of other tetrapods. The tendons of origin make deep grooves on the tibia and are surrounded by a space, the cavum praearticulare of Gaupp. The true cavity of the knee joint lies posterior to these structures. The collateral ligaments are both strong bands, the tibial ligament showing a crossing of its fibres, while the knee-joint cavity is prolonged between the ligament and a facet on the femur.

The two menisci are firmly united both anteriorly and posteriorly. The medial meniscus is attached to the tibio-fibula by an anterior menisco-tibial ligament, while posteriorly both are attached to the intercondylar region of the tibia. Laterally, a small menisco-femoral ligament connects the lateral meniscus with the femur. The expanded tendon of origin of the m. peroneus is attached near its lateral margin to the lateral meniscus. This part of the tendon was described by Gaupp as an anterior cruciate ligament, but it cannot be compared with the structure so called in other animals. Posteriorly the m. semimembranosus entirely, and the m. plantaris longus in part, are attached to the menisci. There is but one cruciate ligament, a large wide mass of fibrous tissue surrounded by the joint cavity on all sides. This single ligament seems to correspond to the double or triple structure found in other tetrapods. Possibly the splitting of a single matrix into two or more ligaments is related to rotary movements, in which the ligaments are twisted on one another, for where there is but one ligament, as in Chelonia and Anura, rotary movements are minimal.

It is clear that the two surviving subclasses of Amphibia possessing limbs (Urodela and Anura) are both highly specialized, though along divergent lines. The probable phylogenetic changes that have occurred are discussed later.

## THE KNEE JOINT IN PRIMITIVE TETRAPODS

To summarize in concrete terms our conclusions as to the probable constitution of the early tetrapod knee joint from which all modern types have been derived, the knee of *Eryops*, an extinct amphibian, is figured. The bones were modelled from the well-known skeleton in the American Museum of Natural History, of which there are casts in the British Museum and at St Thomas's Hospital Medical School (Prof. Appleton's collection), but the positions of the bones have been altered considerably in the model.

As regards the ligaments and menisci there are two main possibilities. *Eryops* may have had these structures but poorly developed, as in modern urodeles. Indeed, Bland Sutton (1884, etc.) supposed that such a simple joint was the ancestral form directly inherited by those modern animals which still possess it, and Lubosch (1910), while recognizing the possibility of a neotenic structure in many amphibians, on the whole agrees with this suggestion. Again, Carleton (1941) speaks of free diarthrodial joints and menisci

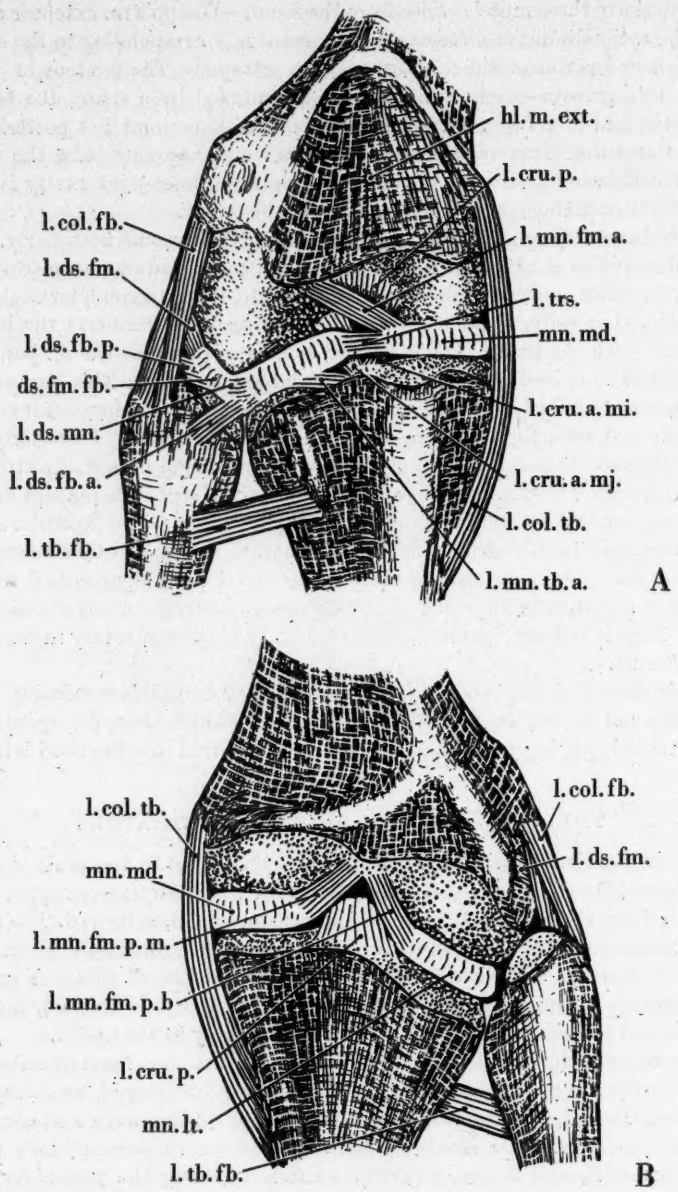


Fig. 6. Reconstruction of the knee of *Eryops megacephalus*.
A, anterior view. B, posterior view.

as new developments in the knee joints of reptiles. On the other hand, Schwarz (1935), working on the wrist joint, recognized that the possession of a joint cavity in urodeles is a primitive feature. Further, the Anura do possess a set of ligaments and menisci similar to those of reptiles, so that unless these structures have been independently developed by parallel evolution, they must have been found in the common ancestors of these groups (Reptilia and Anura), which would also include the ancestors of the Urodela. Thus, in the structure of their joints, as in so many other points of their anatomy, the urodeles would appear to be secondarily simplified rather than truly primitive. These considerations, taken with the shape of the bones in *Eryops*, justify the use of such reptiles as *Crocodilus* and *Sphenodon* rather than any living amphibian as bases for the reconstruction.

If this type of reconstruction rather than one based on modern urodeles is correct, we must abandon hope of understanding the evolution of the menisci and of the main ligaments until fresh fossil material is discovered, for the last common ancestors of all known tetrapods appear to have possessed already a full complement of these structures. Bland Sutton's (1884, etc.) suggestion, for instance, that the collateral ligaments have been derived from the tendons of the adductor magnus and the peroneus longus must be abandoned, for, as Keith (1894) points out, they are well marked in frogs, and there is no embryological support for the theory in mammals.

### *GALLUS DOMESTICUS*

In the domestic fowl the femur shows a wide groove for the large bony patella. On the lateral condyle is a narrow groove, occupied partly by the tendons of the long extensor muscle and partly by the fibula and disc, according to the degree of flexion of the joint. The tibia has an enormous ridge and crest for the insertion of the patellar tendon and origin of the extensor muscles. Posterior to these is a wide hollow occupied in life by an infrapatellar pad of fat, while the articular surface proper is confined to the posterior half of the upper surface.

There is a single joint cavity which extends above the patella, and below overlies the origin of the anterior cruciate ligament. Posteriorly it extends a little on to the shafts of the tibia and fibula. Besides the usual communication of the sections of the cavity above and below the menisci through the central part of the joint around the cruciate ligaments, the two sections also communicate between the tibial collateral ligament and the medial meniscus, in the groove between the two menisci posteriorly, and by way of the femorofibular joint. Besides the tendon of the long extensor, each of the two cruciate ligaments, the posterior menisco-femoral ligament and the posterior tibiofibular ligament all lie quite freely in the joint cavity. Probably this is the largest collection of intra-articular structures known in any joint. In the anterior part of the joint two or three strands similar to the ligamentum

mucosum of mammals may pass from the femur or the tissue above the patella to the intrapatellar pad, but how constant these may be has not been determined.

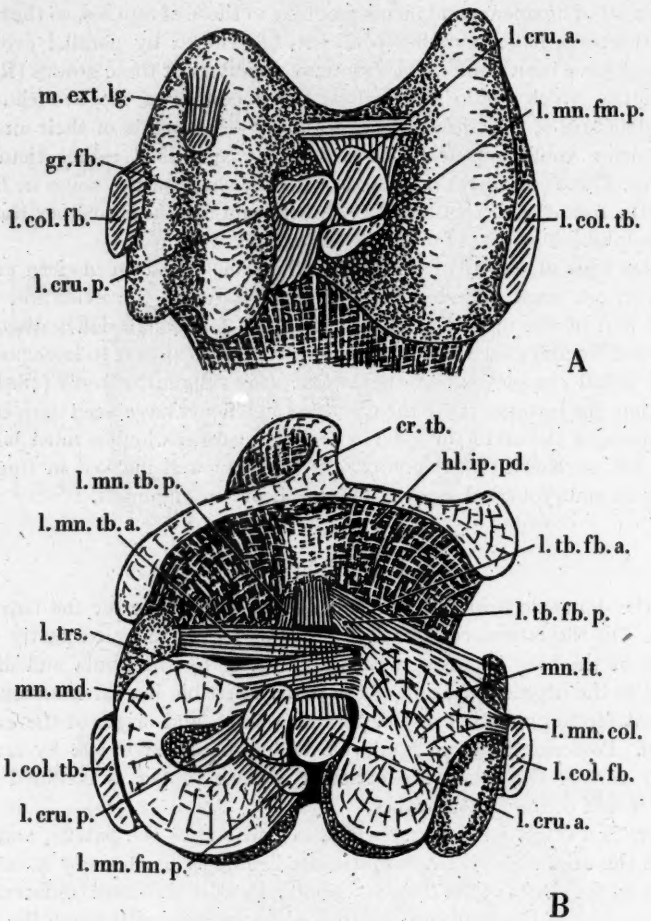


Fig. 7. Knee of *Gallus domesticus*. A, articular surface of femur. B, articular surfaces of tibia and fibula, with menisci.

The collateral ligaments have the usual arrangements. There are only two cruciate ligaments, and the tibial attachment of the anterior of these has been carried relatively far forwards, so as to lie anterior to the articular surface of the tibia. Near this attachment the anterior tibio-fibular ligament passes laterally to the anterior part of the head of the fibula, and a third

ligament, the posterior tibio-fibular, passes from the same region of the tibia through the joint cavity to reach the more posterior part of the head of the fibula, near the medial margin of the articular surface. The menisci are massive structures, the medial C-shaped and the lateral discoidal. Anteriorly they are connected together by a transverse ligament, and the lateral is attached to the tibia by a long anterior menisco-tibial ligament. Posteriorly the medial meniscus is attached to the femur by a posterior menisco-femoral, and by a long posterior menisco-tibial which is attached to the tibia near the anterior cruciate ligament. The lateral meniscus is not attached to either femur or tibia posteriorly, but forms a deep, mobile structure attached to the fibula by a small ligament. The femoro-fibular disc may be represented by a narrow triangular wedge of tissue attached by its base to the lateral meniscus and by its apex to the fibular collateral ligament.

Clearly the avian knee joint is a highly specialized structure, though easily derivable from a reptilian form. The joint gives an impression of rigidity, the ligaments appearing more taut than in other animals examined, and allowing less rotation. In its most posterior part the groove for the fibula turns rather medially, so in extreme flexion the upper end of the fibula is pressed towards the tibia, and the posterior parts of the menisci approach each other. The functional significance of these arrangements needs further study.

It may be noted that, as in mammals, the weaker of the pair of anterior cruciate ligaments found in reptiles has been lost, so that only one anterior and one posterior ligament remain. These ligaments bring about a rotation or 'locking' during extension, but again, as in mammals, this movement is a result of the crossing of the pair of cruciate ligaments and does not seem to serve any particular purpose (Haines, 1941). The account given here agrees with that of Kaupp (1918), but the photographic illustrations there used do not show the ligaments clearly. Again, my account of *Gallus* agrees well with that of Tiedemann (1810) for birds in general.

## MONOTREMATA

In *Echidna* the knee joint is extremely specialized, but retains the femoro-fibular articulation. The lower end of the femur forms, as a whole, a half-cylinder, the surface for the patella and the articular surfaces of the two condyles all conforming to the same simple curvature. The tibia has two rather flat condyles, and an articular surface on its lateral margin for the fibula. The patella is wide from side to side and is concave posteriorly to fit the cylindrical femoral surface. It is held in place by two ligaments, a patello-femoral and a patello-fibular, which pass respectively to the femur and to the expanded upper end of the fibula.

There are two joint cavities. The smaller lies between the medial condyles of the femur and tibia, while the larger, between the lateral condyles, extends between the fibula and the fibular surfaces of the femur and tibia, and,

through a very narrow communication, becomes continuous with the cavity between the femur and patella. Apart from this opening, the three parts of the knee-joint cavity are separate, a thin horizontal septum dividing the patellar cavity from the condylar cavities, while a thick mass of connective tissue, in which the cruciate ligaments are embedded, forms an unbroken antero-posterior septum between the condylar cavities.

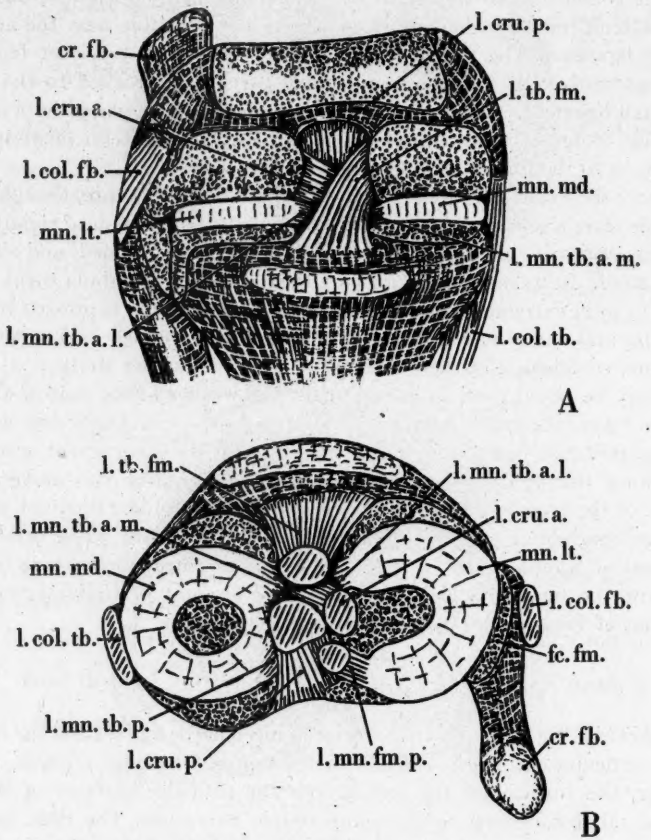


Fig. 8. Knee of *Echidna* sp. A, anterior view, flexed. B, articular surfaces of tibia and fibula, with menisci.

The menisci are thin structures, poorly developed as compared, for example, with *Didelphys*, the medial being circular and the lateral C-shaped. There is no trace of a femoro-fibular disc. The intercondylar margins of the menisci are attached to the tibia, except the posterior horn of the lateral meniscus which is attached to the femur by a posterior menisco-femoral ligament which

follows the course of the posterior cruciate. The two cruciate ligaments are arranged as usual, but in addition to these a large tibio-femoral ligament passes from the tibia to the medial condyle.

This description agrees well with that of Parsons (1900) for the joint cavities, though in his specimen both menisci were C-shaped and the posterior horn of the medial meniscus was attached to the femur. He describes the tibio-femoral ligament as a split-off part of the anterior cruciate, but the true anterior cruciate is attached behind the menisci. It therefore seems more likely that this peculiar ligament is a derivative of the reptilian anterior menisco-femoral and menisco-tibial ligaments which have lost their connexion with the meniscus and have joined together to form a single ligament peculiar to monotremes.

The knee joint of *Ornithorhynchus* is very similar in arrangement to that of *Echidna*, the peculiarities of the bony surfaces and of the patellar and the femoro-tibial ligaments in that animal being repeated. Again, the patello-femoral part of the joint cavity is almost isolated from the condylar parts, but the small communication present in my specimen is with the medial part of the joint, not with the lateral as in my *Echidna*. In Parsons's (1900) animal the patellar cavity was wholly isolated from both of the condylar cavities. Probably these communications are variable even in the same species, and, as suggested later, no phylogenetic conclusions should be drawn from the arrangement of the joint cavities in monotremes.

### *DIDELPHYS VIRGINIANA*

There is in *Didelphys* but one synovial cavity for the knee joint. Anteriorly it is prolonged behind the patella to form a small 'supra-patellar bursa', and posteriorly it forms a small supracondylar sac. Laterally it is continuous with the cavity between the proximal ends of the freely movable tibia and fibula.

Within the joint are four distinct fibro-cartilages, two large femoro-tibial menisci, a small tibio-fibular meniscus and a femoro-fibular disc. The horns of the menisci are attached by ligaments to the tibia, save the posterior horn of the lateral meniscus, which is attached instead to the lateral side of the medial femoral condyle by a posterior menisco-femoral ligament. The tibio-fibular meniscus is a small wedge-shaped fibro-cartilage lying in the anterior part of the superior tibio-fibular joint and occupying about a third of its extent. It is attached above to the ligament which unites the lateral meniscus and disc, and below to the shaft of the tibia.

The disc is a pad of fibro-cartilage articulating with the lateral condyle of the femur above and with the proximal end of the fibula below, and producing a special facet on each of these bones. It is attached anteriorly to the lateral meniscus, and more laterally by a strong disco-femoral ligament to the femur. This latter ligament passes deep to the fibular collateral ligament so that the two structures cross each other in the flexed position of the joint: in extension,

however, the femoral attachment lies behind the fibular collateral ligament and the two ligaments no longer cross. In extreme flexion of the joint the disco-femoral ligament lies in a groove on the lateral femoral condyle, but in other positions the groove is in contact with the synovial surface of the joint

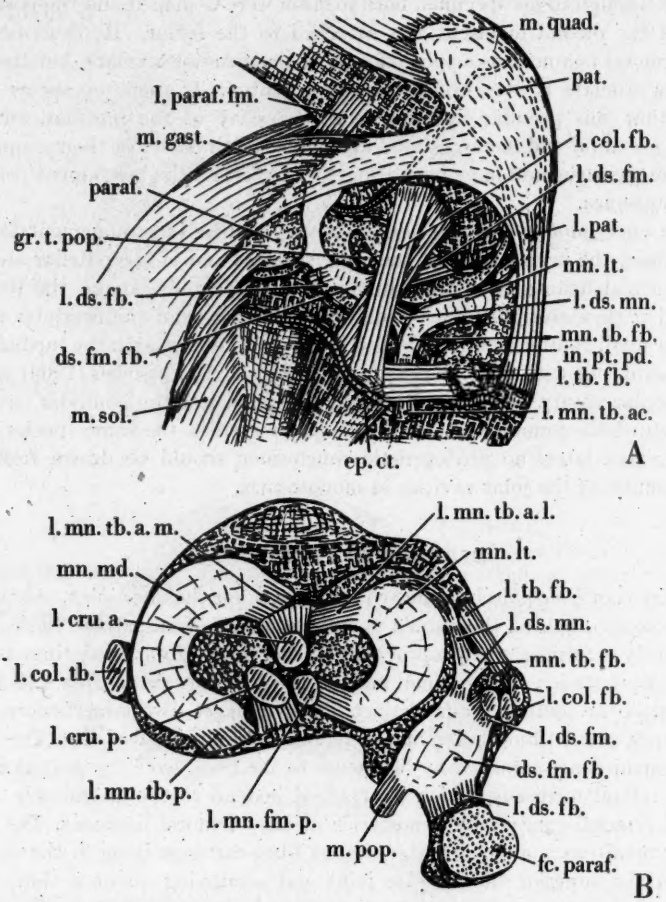


Fig. 9. Knee of *Didelphys virginiana*. A, lateral view, semi-flexed. B, articular surfaces of tibia and fibula with menisci and femoro-fibular disc.

capsule only. Posteriorly the disc is firmly attached by ligament to the head of the fibula, and gives attachment to a tendon by which a part of the popliteus takes origin. The disc and the disco-femoral ligament are intrasynovial structures, the joint cavity separating them from the fibular collateral ligament and the capsule on the one hand, and from the lateral meniscus on the other.

The two cruciate ligaments are attached anterior and posterior to the tibial intercondylar eminence—a well-defined projection, sharply cut on its medial surface where it articulates with the medial femoral condyle. The two cruciate and the menisco-condylar ligaments are completely surrounded by the synovial cavity on their way to their attachment to the intercondylar fossa. The fossa itself contains a little connective tissue and fat surrounding the attachments of the three ligaments. The parafibula is a small conical bone articulating by a synovial joint with the proximal extremity of the fibula, giving part origin to the lateral head of the gastrocnemius and the plantaris. Its apex is attached to the shaft of the femur by a strong femoro-parafibular ligament.

*Movements.* The lateral meniscus is less firmly attached to the tibia than is the medial and can therefore glide over the tibia more freely. The tibial surfaces for the two menisci are roughly equal in size, but the antero-posterior diameter of the lateral meniscus is the smaller, so that it can travel farther without leaving the articular surface. In extension the chief movement occurs between the femur and the menisci, though the menisci, particularly the lateral one, simultaneously glide forwards on the tibia. Rotation occurs fairly freely about an axis through the region of crossing of the cruciate ligaments. The lateral condyle of the femur being wider than the medial and lying farther from the axis of the movement has farther to travel and carries the lateral meniscus with it. The fibula is carried with the tibia, but not so far as would be the case if the two bones were fused, for the superior tibio-fibular joint allows of a considerable antero-posterior gliding movement. Thus, when the leg is rotated medially on the femur, the fibula is dragged forwards by the anterior tibio-fibular ligament, the fibular collateral ligament meanwhile tending to annul its movement. Similarly, when the leg is rotated laterally, the attachment to the femur through the disco-femoral and disco-fibular ligaments tends to prevent movement of the fibula. Thus the movement of the fibula is not conditioned entirely by its femoral attachments, as in lizards, or by its tibial attachments, as in man, but is partly determined by each set of attachments.

This account of *Didelphys* agrees well with that of Parsons (1900) in so far as the larger ligaments and menisci are concerned, but Parsons did not recognize the tibio-fibular meniscus or the disc, so that he supposed the femur and fibula to be in direct contact when the joint was flexed. He described a mechanism whereby, when the tibia and fibula were pressed together by the tibio-fibular musculature, the knee joint became extended with considerable force, and he suggested that the mobility of the fibula was associated with this mechanism, and also compensated for the absence of a bony patella. No such tendency towards extension when the tibia and fibula were pressed together was found in the specimen here described, and the antero-posterior movement of the fibula on the tibia would appear to be associated with movements of rotation rather than with movements of flexion and extension.

Further, the patella would seem to function equally well whether it is bony or cartilaginous, and the quadriceps and femoral origin of the extensor digitorum longus would seem to be as capable of producing extension in marsupials as in other animals. The double origin of popliteus is confirmed by Gruber (1875) in *Didelphys philander*, a specimen of which has been examined and found in all respects similar to *D. virginiana*. Other marsupials examined, and those described in the literature, particularly *Petrogale xanthopus*, figured in detail by Parsons (1896), agree closely with *Didelphys*.

## THE PARAFIBULA AND THE FEMORO-FIBULAR DISC

*Didelphys virginiana* occupied a critical point in the evolutionary scheme proposed by Pearson & Davin (1921) in their work on the sesamoids of the knee. It seemed to these authors that 'in the Marsupialia there had been written the complete history of the lateral sesamoids of the knee joint'. Thus they recorded that in one individual of *Phascolomys* the upper end of the fibula was prolonged as a fibular crest, the supposedly primitive condition; in a specimen of *Sarcophilus* the crest had become partially separated as a parafibula, and in most marsupials they examined (including further individuals of *Phascolomys* and *Sarcophilus*) the parafibula was quite separate. In a specimen of *Didelphys virginiana*, the parafibula had, they considered, divided to form two separate bones, the cyamella and the lateral fabella, corresponding respectively to the sesamoid sometimes found in the tendon of the popliteus and the sesamoid in the lateral head of the gastrocnemius in man. Finally, in *Macropus*, while the fabella had remained bony, the cyamella had failed to ossify and had become a fibro-cartilaginous structure, and in some specimens of *Didelphys* the cyamella had disappeared entirely or almost so.

Now, however, it seems that this series cannot be taken as an evolutionary sequence. The final phase, *Macropus*, shows a bony parafibula and no bony cyamella (Windle & Parsons, 1897), as in our *Didelphys* and as in marsupials in general. Pearson & Davin's *Didelphys*, if it ever possessed a bony cyamella, was peculiar in this feature, but their figure is far from convincing. The typical individuals of *Sarcophilus* and *Phascolomys* again have the usual marsupial structure of the parafibula, a conical bone articulating with a special facet on the fibula, while there is no cyamella. The slight waist noted in the parafibula of *Trichosurus vulpecula* by Pearson & Davin can hardly be taken as evidence of an incipient breaking up into two bones. Again, the single individuals of *Sarcophilus* and *Phascolomys* in which the parafibula is partially or wholly fused with the fibula are to be regarded as peculiar rather than as atavistic in this feature. The femoro-fibular disc of marsupials is clearly derived from the disc of reptiles. On the other hand, the tibio-fibular meniscus is a new structure, for in the reptilian joint there is no articulation between the tibia and fibula.

The parafibula has usually been considered as a large sesamoid in the lateral head of the gastrocnemius, homologous with the lateral fabella of eutherian mammals. We have seen above that Pearson & Davin thought it equivalent to the fabella plus the cyamella, but we have rejected that theory. Banchi (1900,1901), finding the parafibula well developed though in a peculiar position in a 20 mm. embryo of *Pseudochirus* and a 30 mm. *Halmaturus*, suggested that it was not a sesamoid but a remnant of the third ray, equivalent in status to the tibia or fibula. He identified it, however, with the ossification in the femoro-fibular disc of lizards, but, as we have seen, it is the marsupial disc which is homologous with that structure, not the parafibula. Again, the time of appearance of the cartilage seems determined by its size, the eutherian patella for instance appearing relatively early, so that there is no embryological reason to reject the supposition that the marsupial parafibula is an enlarged fabella.

### *SCIURUS CAROLINENSIS*

The grey squirrel is a good and easily obtainable eutherian type, still retaining the size and perhaps something of the habits of the early arboreal ancestors of the Mammalia (Matthew, 1904). The knee joint has some slight modifications that allow for great rotatory mobility, but otherwise its structure seems representative of the general eutherian arrangement.

The single-joint cavity is prolonged without any constriction so as to pass up between the femur and the patella, this last being a double structure with the lower part bony and the upper part fibro-cartilaginous as in many rodents. The superior tibio-fibular joint is, however, quite distinct from the knee joint, and is surrounded on all sides with a continuous capsule. Below the patella is a large infrapatellar pad of fat which fills up the space between the femur, tibia and patellar tendon; but, though its margin lies in contact with the cruciate ligaments, its whole posterior surface is separated from other structures by the joint cavity, which has an antero-inferior extension between the fat and the menisci. Thus, there is no ligamentum mucosum separating the two sides of the femoro-tibial joint.

The collateral ligaments are both long, particularly the tibial ligament. Posteriorly, there are three sesamoids, two fabellae in the tendons of origin of the gastrocnemius, and a cyamella in the tendon of popliteus. Each has a small cartilage-covered articular facet; the fabellae articulate with the condyles of the femur and the cyamella with the lateral condyle of the tibia. Apart from these facets related to the cavity of the knee joint, the surface of each sesamoid is covered with muscular and tendinous tissue. The tendon of the popliteus above the sesamoid is completely surrounded by the cavity of the knee joint as far as its attachment at the anterior end of the groove on the femur.

The menisci are both well-developed C-shaped fibro-cartilages. Their anterior ends are attached by long menisco-tibial ligaments to the tibia,

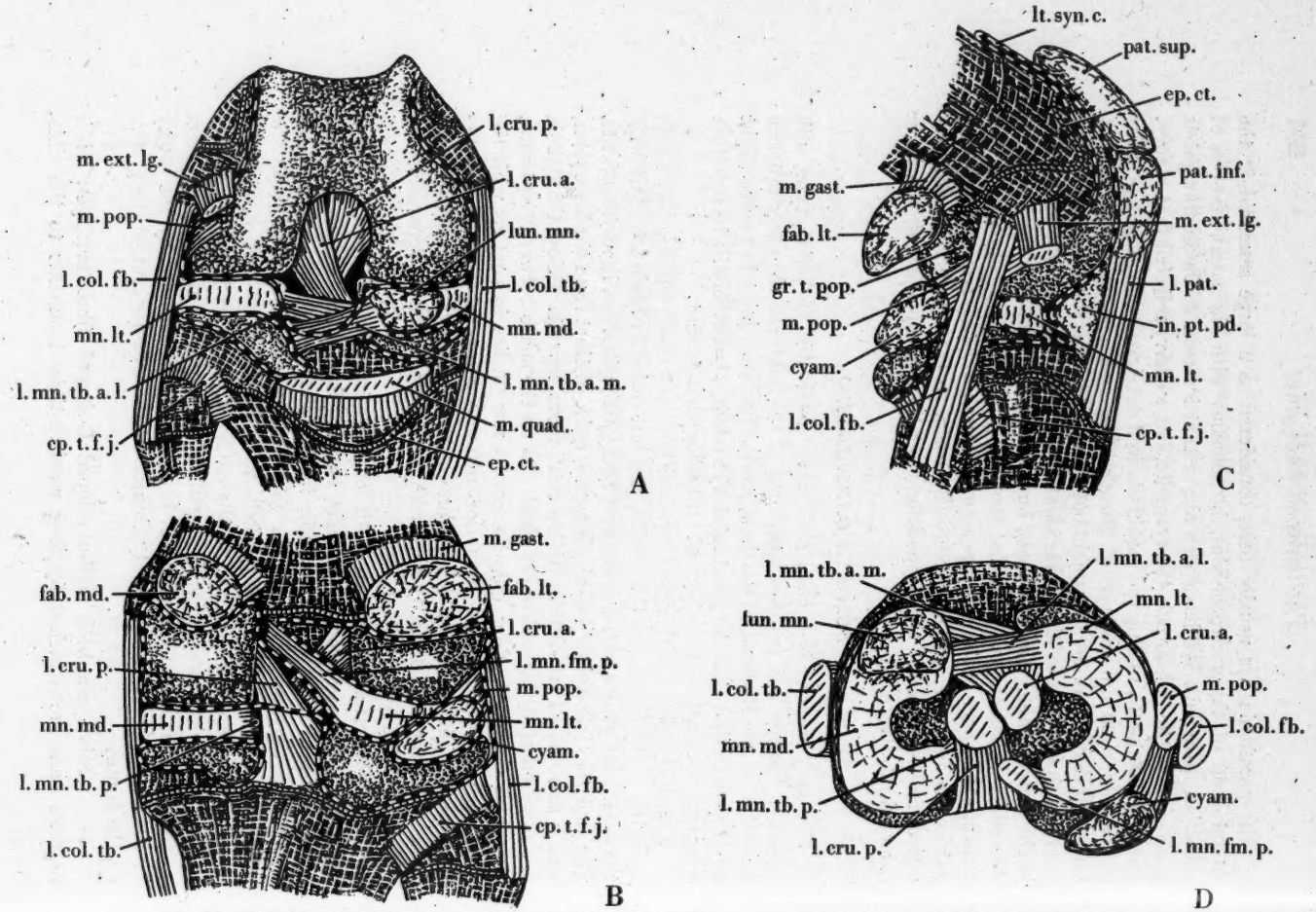


Fig. 10. Knee of *Sciurus carolinensis*. A, anterior view, flexed. B, posterior view, extended. C, lateral view, semi-flexed. D, articular surface of tibia with menisci.

that from the medial meniscus lying anterior to that from the lateral, an arrangement found by Parsons (1898) in *Pedetes*. The posterior end of the medial meniscus is attached by a short ligament to the tibia, that of the lateral by a longer ligament to the femur. There is an antero-medial lunula in the medial meniscus.

The two cruciate ligaments are joined by loose connective tissue, the two together being surrounded by the joint cavity to form an intrasynovial structure. The anterior cruciate ligament is attached behind the anterior menisco-tibial ligaments, the posterior to the posterior margin of the articular region of the tibia.

Compared with the joints previously described there is, during flexion and extension, more antero-posterior movement of the menisci over the tibia, the position of the femur on the tibia being determined as usual by the cruciate ligaments, and the menisci being driven backwards and forwards by the femur. Rotation is very free, both the collateral ligaments being long, particularly the fibular, and the length of the anterior menisco-tibial ligaments also allows of the free independent movements of the menisci as the condyles of the femur pass backwards and forwards in rotation, carrying the menisci with them. Apart from this exaggerated rotation, the knee joint of *Sciurus* agrees well with the usual mammalian type discussed by Parsons (1900).

## THE SYNOVIAL CAVITY OF THE TETRAPOD KNEE JOINT

Bland Sutton (1884, etc.) suggested that the primitive mammalian knee joint had three separate cavities, as in the beaver (*Castor*), one between the patella and femur, the other two between the condyles of the femur and of the tibia. He considered the ligamentum mucosum and the alar ligaments of man to be remnants of the septa between these primitive cavities. In man again Bland Sutton supposed that a fourth element, a bursa lying beneath the quadriceps, which in the third month of foetal life had but a small communication with the patellar part of the joint, became incorporated into the joint cavity as growth proceeded. This theory of the multilocular derivation of the knee-joint cavity also appears in the name rudimentum septi given to the connective tissue in which the cruciate ligaments are embedded, together with the ligamentum mucosum when it is present. Again, Bland Sutton himself, since he considered most ligaments to be the divorced tendons of muscles, made no suggestion as to the derivation of the cruciate ligaments, but it has been suggested that these were originally collateral ligaments of the condylar joints when these were still separate, a point mentioned but not supported by Fick (1910).

Parsons (1900) summarizes conditions in mammals by saying that the rudimentum septi 'may be (1) quite unconnected with the femur as in the lemur; (2) slightly connected with it as in man; (3) forming an antero-posterior partition between the two condylar joints, as in most monkeys and the otter;

Fig. 10. Knee of *Sciurus carolinensis*. A, anterior view, flexed. B, posterior view, extended. C, lateral view, semi-flexed. D, articular surface of tibia with menisci.

(4) completely separating the knee into three cavities, two condylar and one trochlear, as in the three-toed sloth and duck-mole; (5) separating the joint into two unequal parts, one trochleo-condylar and the other condylar, as in the brocket deer'. From this admirable summary Parsons himself drew no conclusions as to which form was the most primitive, but Fick (1910) remarked that it by no means confirmed Bland Sutton's theory, since in the lemur, a relatively primitive form, the knee joint was quite undivided.

Now in reptiles the two condylar cavities are connected with each other in front of, behind and often between the cruciate ligaments, and the knee-joint cavity is always continued as a femoro-fibular joint. Extension of the joint proximally may have occurred, as suggested by Bland Sutton, by the formation of a separate bursa deep to the quadriceps tendon or the patella, for in *Emys* such a bursa is found. In those reptiles, however, which resemble the mammals in having large epiphyses with secondary centres (*Sphenodon*), or which have in addition a bony patella (lizards), there is no subdivision of the knee-joint cavity. Again in lizards and birds the cavity has extended farther to include the tendon of origin of the long extensor muscle, and it seems most probable that the whole of the reptilian cavity is derived phylogenetically from a single original cavity without the addition of bursae.

In mammals there is always a certain amount of connective tissue within the joint, and well-developed septa are known in primates, carnivores, ungulates, edentates, insectivores and monotremes, while a ligamentum mucosum has been described in the marsupial *Petrogale* (Parsons, 1896). The more complete septa are found in the larger rather than in the smaller members of these orders, *Castor* as opposed to *Sciurus*, *Macaca* as opposed to *Lemur* (Parsons, 1900), *Bos* as opposed to *Sus* (Sisson & Grossman, 1938), though some small animals such as *Chrysochloris* (Parsons, 1901) have the knee joint subdivided. It is difficult to be certain what the primitive mammalian state may have been and how far a similarity in the arrangement of the joint cavities in (say) monotremes and horses is due to parallel evolutionary development. But from a study of reptiles it seems quite certain that there was originally but one joint cavity in tetrapods.

Now the effect of the subdivision of the knee joint is to clothe the originally intrasynovial structures such as the cruciate ligaments, and also parts of the originally free joint surfaces of the bones, with connective tissue, and this connective tissue carries blood vessels. In lizards the cruciate ligaments lie freely in the synovial cavity, and, as has been confirmed by microscopic examination, have no blood supply whatever, so that their nutrition is derived from the synovial fluid. The covering of connective tissue in typical mammals provides a direct blood supply to the structures in the interior of the joint, and allows the ingress of proprioceptive nerves. There may of course have been other, unknown, functional influences affecting these developments.

In primitive tetrapods the extent of the cavity of each joint probably corresponded to the extent of the uncalcified cartilaginous epiphyses

(Haines, 1938), and so to the margin of the bony shaft, and there were no intrasynovial muscle attachments, a set of conditions still found in *Crocodilus*. In more specialized types the joint cavity might extend over the shaft, as in the supracondylar extension at the back of the joint in *Sphenodon*. On the other hand, in animals with large epiphyses having their own centres of ossification, such as lizards and mammals, the osteogenic tissues and blood vessels which supply the secondary centres of ossification are derived from the perichondrium, so that some part of the surface area of each cartilaginous epiphysis must be covered with perichondrium and not with articular cartilage. The development of connective tissue septa within the joint still further complicates the relations of the joint cavity to the epiphysial line.

The development of the cavities of the knee joint in man has been studied by Langer (1929) by the method of reconstruction models. He found at 37 mm. four cavities, two related to the condyles and two to the patella, and showed how these cavities later spread around the menisci and joined to form the single cavity of the adult. Though the development in other species is not known in detail, it appears to be similar, and to account for the variations found in the number and arrangement of the cavities in individuals of the same species, for instance the horse and ox (Sisson & Grossman, 1938). The histological changes have been studied by many authors, and seem very similar in birds and mammals (Hepburn, 1889; Fell, 1925). The actual formation of the septa in mammals presumably depends on a secondary failure of union of the separate cavities found in the embryo, leaving a mesenchymal matrix later vascularized to form the adult structures.

The tibio-fibular cavity has been derived from that of the knee joint. In reptiles the fibulo-femoral articulation is a part of the joint, but the fibula does not touch the tibia, while in monotremes the fibula articulates with both femur and tibia. Probably the eutherian mammals passed through some such stage before the femoro-fibular articulation was lost, while the tibio-fibular persisted. So the connexion between the tibio-fibular joint and the main cavity of the knee joint, found in some mammals, is a remnant of a more primitive, ancestral continuity (Parsons, 1900).

## MECHANISM OF THE KNEE JOINT IN REPTILES AND MAMMALS

In reptiles and mammals the arrangements for flexion and extension, and the functions of the collateral and cruciate ligaments, are very similar, but the mechanism of rotation is quite different. In reptiles such as crocodiles and lizards the tibia and fibula are not attached to each other by any strong interosseous membrane or ligaments apart from the superior tibio-fibular ligament already described. At its lower end each bone is firmly attached to the tarsus by a hinge joint with rather limited movement, for the main mobility of the region is provided by the intertarsal joints; in the line leading to birds the ankle joint is lost altogether as a result of the formation of a tibio-tarsal

bone (Vialleton, 1924). Now, at the ankle joint there is no appreciable rotation, so that when the foot is rotated relatively to the femur the tibia and fibula rotate with it, but at the same time they are free to move anteroposteriorly relatively to each other by flexion of the tibia on the tarsus with extension of the fibula, or vice versa.

At any particular degree of flexion of the knee joint the positions of the upper ends of the tibia and fibula are rigidly determined, for each bone is held in place, the tibia chiefly by the cruciate ligaments, and the fibula by the hollow in the femur in which it is held by its ligamentous attachments, but at the same time each bone is free to rotate about its own axis. So when

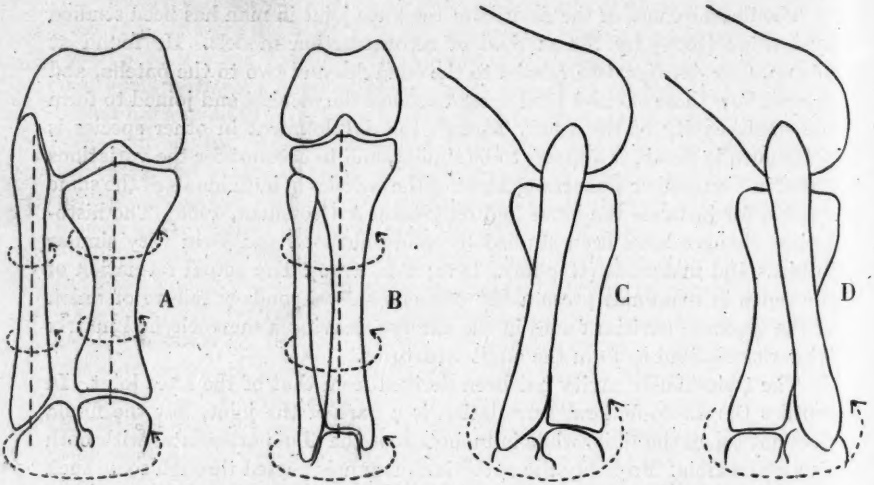


Fig. 11. Diagrams showing mechanism of rotation in a reptile and a eutherian mammal. A, rotation of foot in reptile, anterior view. B, rotation of foot in mammal, anterior view. C and D, rotation of foot in reptile, lateral view.

the foot is rotated the tibia and fibula each rotate on the femur, but separately, each about its own axis (Fig. 11 A). The fixation of the ends of the tibia and fibula to the femur on the one hand and to the tarsus on the other enforces some mutual displacement of the bones relatively to each other during rotation (Fig. 11 C, D), as does the similar fixation of the radius and ulna in man, but whereas in the human forearm the ulna rotates with the humerus and the radius with the carpus, in the reptilian leg both tibia and fibula rotate with the tarsus alone.

Carleton (1941) suggests that 'in reptiles, as in amphibia, rotational action of the lower part of the hindlimb is produced almost entirely by muscles acting on the tarsal joints', that there is little relative movement between the tibia and fibula, and that the muscles which pass between these two bones

serve only to prevent their separation by the pull of the other muscles. There seems, however, to be nothing in the shape or arrangement of the bones of *Trematops* or *Ophiacodon*, the forms chosen for the study of the primitive type of hindlimb, to prevent movements such as those described above. Further, I would associate the musculature passing between the tibia and fibula with relative movements of these two bones. It is true that, as Carleton points out, the attachment of this musculature is to the lateral aspect of the tibia, and not across the bone to its medial border as might be expected from a comparison with the pronator teres of the forelimb. But, as shown above, the movements of the tibia and fibula are unlike those of the radius and ulna, and a different arrangement of the musculature is therefore to be expected.

In typical eutherian mammals the ankle has become a very mobile hinge joint. The tibia and fibula have accordingly approached each other so as to form a deep socket for the talus, and movements between them have become minimal. In association with this the fibula has become shorter so as to lose its femoral attachment, and has gained a new attachment to the upper end of the tibia, so that during rotation there is no need for mutual displacement of the tibia and fibula with possible interference with the ankle joint (Fig. 11 B). The bones are now closely bound together by the interosseous membrane and the ligaments, and it makes little difference to the mechanism of rotation if they are actually fused. Again, with the loss of independent movement the deeper musculature between the tibia and fibula has disappeared, probably taking a part in the formation of the interosseous membrane, while the popliteus has acquired a new attachment to the femur.

Marsupials occupy an intermediate position in these changes, for the fibula still moves to a large extent with the femur rather than with the tibia, the superior tibio-fibular joint is still a part of the knee joint, the femoro-fibular disc has the reptilian arrangement, and the popliteus does not reach the femur. But these conditions, as also the addition of the disco-femoral ligament to the popliteal tendon and the ossification of the discus to form the cyamella, have been adequately discussed by Fürst (1903) and by Taylor & Bonney (1905) and need not be detailed here. The actual amount of rotation has according to Carleton (1941) never been much greater in man's ancestors than in living man, where it has been measured by Ross (1932) and others.

The detailed mechanism of the knee joint in frogs, where somewhat similar changes have occurred, needs further study.

## LUNULAE

Ossicles in the semilunar cartilages are known in *Sphenodon*, in lizards, including fossil varanids (Nopsca, 1903), and in many mammals. Pearson & Davin (1921), who have given an excellent account of their distribution in lizards and mammals, failed to understand their relation to the semilunar cartilages, and considered them as sesamoids, equivalent in value to the fabellae found in the heads of the gastrocnemius. Leydig (1872), who found

three of these ossicles in *Lacerta*, was quite clear as to their position in the cartilages, and this has been confirmed by my own sections of numerous lizards and mammals (Haines, 1940). Probably they are developed whenever a semilunar cartilage reaches a certain critical size in any particular species.

Another ossicle of this group is found in the femoro-fibular disc of all lizards, and this also was noted by Leydig. As has been seen, the femoro-fibular disc very probably became the sesamoid in the popliteus of eutherian mammals, but it would seem unwise to call the reptilian structure a cyamella on that account. Both Banchi (1900) and Pearson & Davin (1921) associate the lacertilian ossicle with the parafibula of marsupials, with which it actually has no relation. It seems preferable to speak of a derivation of a lacertilian femoro-fibular lunula and of a mammalian cyamella from the femoro-fibular disc which formed part of the ancestral heritage of tetrapods.

## SUMMARY

1. The most primitive type of knee joint found in living animals is seen in *Crocodilus*. There is a single-joint cavity for the femur, tibia and fibula, and the cruciate and collateral ligaments, the menisci and the femoro-fibular disc are all well developed. A reconstruction of the knee joint of an early tetrapod *Eryops* resembles *Crocodilus* very closely.

2. In *Sphenodon* and lizards the joint is similarly constructed, but the cavity has extended over the shafts of the bones, and ossifications of the semilunar cartilages, the lunulae, are found.

3. In chelonians such as *Emys* the joint is specialized by the formation of a very firm articulation between the medial condyle of the femur and the tibia, with a reduction of the medial meniscus.

4. All modern amphibians have highly specialized joints, the urodeles having lost the joint cavity in whole (*Megalobatrachus*) or in part (*Salamandra*), and having also lost the cruciate ligaments and menisci, while the anurans have lost the femoro-fibular articulation, but retain the ligaments and menisci.

5. In birds such as *Gallus* the knee joint is specialized but is easily derivable from a reptilian form.

6. The monotremes retain the femoro-fibular articulation, but the lower surface of the femur has become reshaped to form a simple roller, while the joint cavity has become secondarily subdivided by septa of connective tissue.

7. In marsupials the structures found in reptiles are all preserved, but there is a new contact of the upper end of the tibia with the fibula to form a gliding joint which allows considerable movement of the two bones on each other. The marsupial parafibula is a sesamoid bone in the gastrocnemius, and has nothing to do with the origin of the cyamella.

8. The connective tissue septa found partially or completely subdividing the knee joints of some mammals are not primitive structures, but are parts of the embryonic mesenchyme retained in the interior of the joints to carry blood vessels and nerves to the intra-articular structures.

9. In typical reptiles the tibia and fibula are not attached to each other by joints or by interosseous membranes, and during rotation of the foot each bone rotates independently on the femur, and there is a large musculature passing between the tibia and fibula. In eutherian mammals the fibula has lost its contact with the femur and has become firmly bound to the tibia, primarily to form a deep socket for the talus at the ankle joint, so that during rotation it moves with the tibia rather than with the femur, and the tibiofibular musculature has partly disappeared and partly altered its position. The marsupials occupy an intermediate position in these respects.

10. Lunulae are ossifications developed in the semilunar cartilages and are not of the nature of sesamoid bones.

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## KEY TO LETTERING

| | |
|---|---|
| *bur.sc.* | sub-crureal bursa |
| *cap.fm.* | capitulum femorale. |
| *cnd.lt.* | lateral condyle. |
| *cp.t.f.j.* | capsule of tibio-fibular joint. |
| *cr.fb.* | crest of fibula. |
| *cr.tb.* | crest of tibia. |
| *cyam.* | cyamella. |
| *ds.fm.fb.* | discus femoro-fibularis. |
| *ep.ct.* | epiphysial cartilage. |
| *fab.lt.* | fabella lateralis. |
| *fab.md.* | fabella medialis |
| *fc.fm.* | facet for femur. |
| *fc.paraf.* | facet for parafibula. |
| *gr.fb.* | groove for fibula. |
| *gr.t.pop.* | groove for tendon of popliteus. |
| *hl.cap.* | hollow for capitulum. |
| *hl.ip.pd.* | hollow for infrapatellar pad. |
| *hl.m.ext.* | hollow for extensor musculature. |
| *in.pt.pd.* | infrapatellar pad of fat. |
| *l.col.fb.* | ligamentum collaterale fibulare. |
| *l.col.tb.* | ligamentum collaterale tibiale. |
| *l.cru.* | ligamentum cruciatum. |
| *l.cru.a.* | ligamentum cruciatum anterius. |
| *l.cru.a.mi.* | ligamentum cruciatum anterius minus. |
| *l.cru.a.mj.* | ligamentum cruciatum anterius majus. |
| *l.cru.p.* | ligamentum cruciatum posterius. |
| *l.ds.fb.* | ligamentum disco-fibulare. |
| *l.ds.fb.a.* | ligamentum disco-fibulare anterius. |
| *l.ds.fb.p.* | ligamentum disco-fibulare posterius. |
| *l.ds.fm.* | ligamentum disco-femorale. |
| *l.ds.mn.* | ligament connecting femoro-fibular disc and meniscus. |
| *l.ds.tb.* | ligamentum disco-tibiale. |
| *l.mn.col.* | ligament attaching meniscus to collateral ligament. |
| *l.mn.fb.a.* | ligamentum menisco-fibulare anterius. |
| *l.mn.fb.p.* | ligamentum menisco-fibulare posterius. |
| *l.mn.fm.a.* | ligamentum menisco-femorale anterius. |
| *l.mn.fm.a.mi.* | ligamentum menisco-femorale anterius minus. |
| *l.mn.fm.a.mj.* | ligamentum menisco-femorale anterius majus. |
| *l.mn.fm.p.* | ligamentum menisco-femorale posterius. |
| *l.mn.fm.p.l.* | ligamentum menisco-femorale posterius laterale. |
| *l.mn.fm.p.m.* | ligamentum menisco-femorale posterius mediale. |
| *l.mn.tb.a.* | ligamentum menisco-tibiale anterius. |
| *l.mn.tb.a.l.* | ligamentum menisco-tibiale anterius laterale. |
| *l.mn.tb.a.m.* | ligamentum menisco-tibiale anterius mediale. |
| *l.mn.tb.ac.* | ligamentum menisco-tibiale accessorius. |
| *l.mn.tb.p.* | ligamentum menisco-tibiale posterius. |
| *l.paraf.fm.* | ligamentum parafibulo-femorale. |
| *l.pat.* | ligamentum patellae. |

| | |
|---|---|
| *l.tb.fb.* | ligamentum tibio-fibulare. |
| *l.tb.fb.a.* | ligamentum tibio-fibulare anterius. |
| *l.tb.fb.p.* | ligamentum tibio-fibulare posterius. |
| *l.tb.fm.* | ligamentum tibio-femorale. |
| *l.trs.* | ligamentum transversum. |
| *lt.syn.c.* | limit of synovial cavity. |
| *lun.ds.* | lunula in disc. |
| *lun.mn.* | lunula in meniscus. |
| *m.ext.c.b.* | musculus extensor cruris brevis. |
| *m.ext.lg.* | long extensor muscle. |
| *m.fl.int.* | intercapital flexor musculature. |
| *m.gast.* | musculus gastrocnemius. |
| *m.per.* | musculus peroneus. |
| *m.plant.l.* | musculus plantaris longus. |
| *m.pop.* | musculus popliteus. |
| *m.quad.* | musculus quadriceps. |
| *m.s.mem.* | musculus semimembranosus. |
| *m.sol.* | musculus soleus. |
| *m.tb.a.l.* | musculus tibialis anticus longus. |
| *mn.lt.* | lateral meniscus. |
| *mn.md.* | medial meniscus. |
| *mn.tb.fb.* | tibio-fibular meniscus. |
| *paraf.* | parafibula. |
| *pat.* | patella. |
| *pat.inf.* | patella inferior. |
| *pat.sup.* | patella superior. |
| *s.cnd.s.c.* | supra-condylar extension of synovial cavity. |

# THALAMO-FRONTAL PROJECTION IN MAN

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One of the most striking results of the recent investigations on cortico-thalamic relations (Le Gros Clark, 1936; Walker, 1938) is the fact that developmentally recent cortical 'association' areas receive impulses from discrete thalamic nuclei. This fact had been known vaguely before, but the extent to which such a relationship exists is something new, and must influence our conceptions of the so-called higher cortical functions to a large degree.

All these studies were made on primates and lower mammals, and apart from a few observations (Monakow, 1895; Probst, 1900; Dejerine, 1901; Fukuda, 1919) little is known about these relations in the human brain. It is not easy to find cases appropriate for this type of study, and much of our knowledge concerning the thalamo-cortical connexions in man must be reconstructed from a compilation of single observations like the present one.

## CASE REPORT

The patient was a 63-year-old bricklayer who, until the time of his accident, had enjoyed perfect health. In October 1928 he was hit on the head by a brick; he was brought into the hospital in an unconscious state, with a comminuted fracture in the right fronto-parietal region showing a marked depression. During the operation, which was performed by Dr W. V. Cone under local anaesthesia, the depressed fragments of the skull were removed, and softened brain tissue was removed by light suction and irrigation. The dura was closed and the wound drained through a separate stab wound. The patient improved from the time of the operation onward, and his post-operative course was uneventful apart from the fact that he had an acute state of confusion with disorientation, impairment of memory for recent events, confabulations, delusions and hallucinations. This cleared up so that he was able to be discharged after six weeks.

Inquiring into his condition over several years preceding his death, it was ascertained from his wife that he had had no seizures; he had been somewhat 'nervous' and 'irritable' at times.

In 1936, eight years after his accident, he was admitted to St Luke's Hospital in a state of cardiac decompensation, and died there after a few days. General pathological examination revealed hypertrophy and dilatation of the heart, passive hyperaemia of lungs, liver ('nutmeg' appearance) and kidneys, oedema, and jaundice.

On the right side in the fronto-temporal region there was a large depression of the skull, the skin containing a fine linear scar. There was a loss of bone tissue 3½ in. in diameter and this region was covered by dura, connective tissue, thin strips of muscles, fascia, and skin. The brain weighed 1200 g. It showed a slight asymmetry with a little bulging of the right parietal region laterally (Fig. 1). In the right frontal region was a piece of dura adherent to the underlying cerebral structures over an area of approximately 4·5 × 2·5 cm. This area was sunken in from the surrounding brain. Its postero-inferior angle lay 1 cm. superior to the junction of the vertical and horizontal rami of the right Sylvian fissure. Superior and posterior to the dural attachment was a further area of atrophy over which the leptomeninges were thickened and the cortex very thin, so that on tugging of the dura one saw movements of adjacent thin cortex. No other scarred area could be seen.

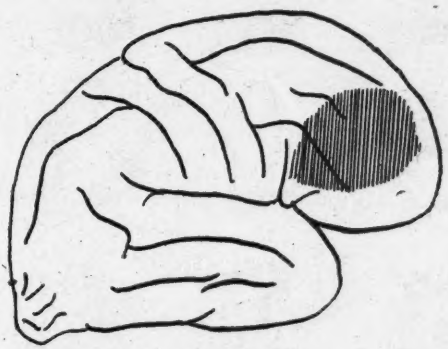

Fig. 1. Lateral aspect of right hemisphere. The lesion is shaded. Traced from photographs.

The base was not unusual, except that the arachnoid here seemed somewhat thickened. The vessels of the base were remarkably free of plaques.

The dura was peeled away from its attachment over the right frontal lobe with surprising ease, revealing a partially opaque membrane overlying what was apparently a cyst. There were no vessels of any size crossing from the dura to the leptomeninges.

The atrophy of the frontal lobe was quite apparent, but in none of the sections was there any ventricular dilatation or distortion. There were cystic areas in the leptomeninges at the site of the dural attachment. Beneath this there were small intracerebral cysts of a light yellowish brown colour. The largest measured 2·0 × 1·0 cm. and had only a thin shell of cortex overlying it. There was considerable alteration of the cerebral tissue beneath the thickened leptomeninges, in addition to the cysts, and some areas had a greyish appearance. The greatest involvement extended 2·3 cm. beneath the brain surface and came to within 0·65 cm. of the right anterior horn. No suggestion of a

cicatrix extending deep into the cerebral tissue was evident. Microscopic examination at the time of the post-mortem examination showed a typical cerebral cicatrix with a great amount of glial and comparatively little mesodermal tissue taking part in the organization. There were still a few fat droplets present in the scar tissue.

When the present study was undertaken the cortical area of destruction had been cut extensively for other purposes so that it was only possible to trace the extent of the lesion from photographs, and from the above protocol (Figs. 1, 2). The basal ganglia were completely preserved. The thalami of

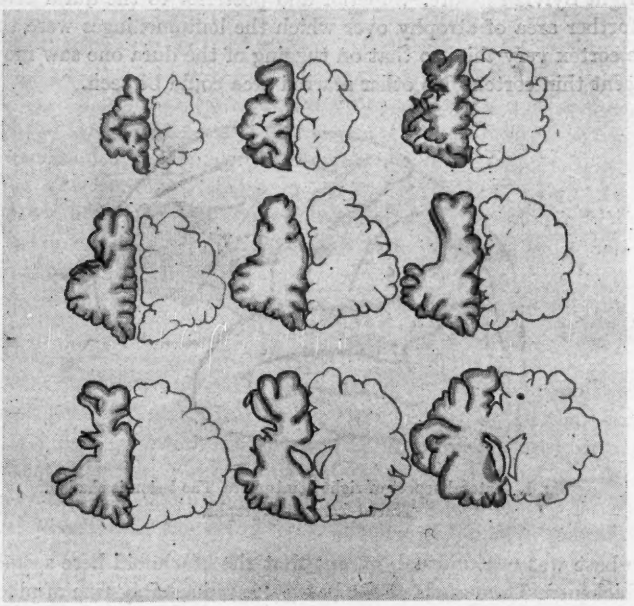

Fig. 2. Coronal sections, traced from photographs and showing the depth of the lesion in the right hemisphere. Of the left hemisphere only the contour is indicated.

either side were embedded separately in celloidin, cut in serial sections (at 20 $\mu$), and every fifth section was stained with thionin.

The left thalamus was completely normal. The right side showed extensive degeneration with either complete loss or considerable rarification of nerve cells accompanied by marked gliosis in the following two areas: the dorsomedial nucleus, and a part of the lateral nuclear mass which would in primates correspond to the ventro-lateral nucleus.[1] The degeneration of the latter extended from the most rostral level of the thalamus back to about the anterior level of the centro-median nucleus. It was confined to the medial

[1] Dr A. E. Walker, who was kind enough to study some representative sections, confirmed this designation.

third of the ventro-lateral nucleus, and there again the most medial parts immediately adjoining the internal medullary lamina were affected most severely, the degree of degeneration gradually diminishing in a lateral direction. In the dorso-medial nucleus the medial part was unaffected, the lateral

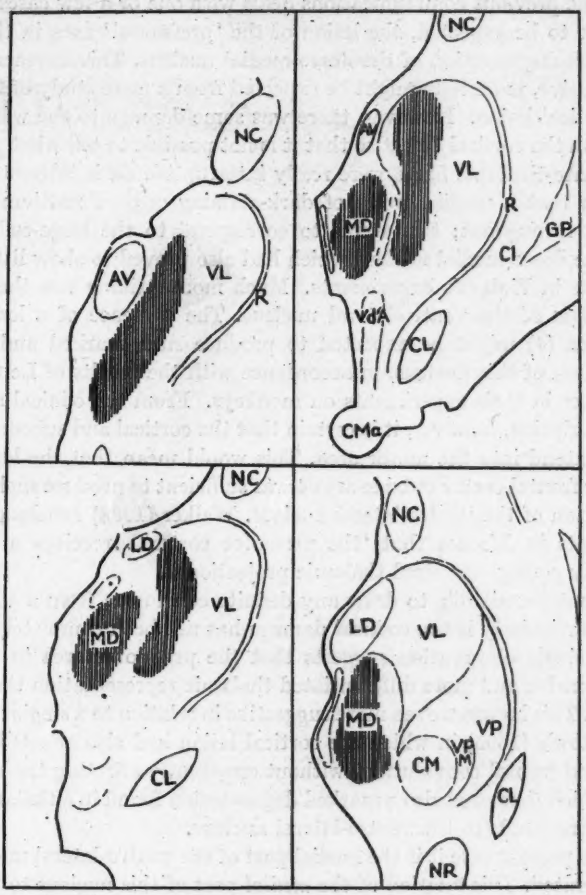


Fig. 3. Camera lucida drawing of right thalamus showing area of retrograde degeneration (shaded). *AV* = n. antero-ventralis, *CI* = capsula interna, *CL* = corpus Luysii, *CM* = centre median, *CMa* = corpus mamillare, *GP* = globus pallidus, *LD* = n. latero-dorsalis, *MD* = n. dorso-medialis, *NC* = n. caudatus, *R* = zona reticulata, *V.d'A.* = tractus mamillo-thalamicus (Vicq d'Azyr), *VL* = n. ventro-lateralis, *VP* = n. ventralis posterior, *V.P.M.* = n. ventralis posterior medialis.

part (small-celled portion?) was affected in the anterior levels almost in its entirety, in the posterior levels more medially and dorsally than laterally and ventrally (Fig. 3).

The remaining parts of the thalamus and of the basal ganglia were normal.

## DISCUSSION

As already mentioned above, observations on the cortico-thalamic relations in man are scanty as compared with the rich experimental literature. Each of the previous communications deals with one or a few cases.

As was to be expected, the lesion of the 'prefrontal' area in the present case caused degeneration of the dorso-medial nucleus. This degeneration was very extensive, more than might be expected from a mere study of the outline of the cortical lesion. However, there was some damage to the white matter underneath the cortical defect so that it is not possible to tell what proportion of the fronto-thalamic fibres were really interrupted. It is interesting in this connexion that a medial group of dark-staining cells of medium size were preserved throughout; this seems to correspond to the large-celled medial part of the dorso-medial nucleus which had also proved to show little cortical connexions in Walker's experiments. Much more striking was the extensive degeneration of the ventro-lateral nucleus. The presence of a lesion in the motor area (4) might be expected to produce such marked and extensive degeneration of this nucleus, in accordance with the results of Le Gros Clark and Walker in their experiments on monkeys. From the clinical and anatomical description, however, it is certain that the cortical and subcortical lesion did not extend into the motor area. This would mean that the lesion of the agranular frontal cortex outside area 4 was sufficient to produce such extensive degeneration of the ventro-lateral nucleus. Walker (1938) concludes from his experiments in *Macaca* that 'the premotor cortex...receives a slight and apparently poorly organized thalamic projection'.

It is not permissible to draw any definite conclusion from a single observation, particularly if the cortical damage has not been completely analysed, but this single observation suggests that the pre-motor area in man has a more extensive and more differentiated thalamic representation than in lower primates. This becomes even more suggestive in relation to a single observation of Monakow's (1895) in which the cortical lesion had also affected 'the third and second frontal convolution' without apparently affecting the motor area, and in which there was also a marked degeneration found in a thalamic nucleus which corresponds to the ventro-lateral nucleus.

In the present case it is the medial part of the ventro-lateral nucleus which is degenerated. This relation of the *medial* part of this nucleus to the *inferior* part of the agranular frontal cortex is comparable to the spatial relation between the motor cortex proper and this nucleus in primates.

## SUMMARY

A case of a traumatic cortical lesion of the 'prefrontal' and 'premotor' areas was studied for retrograde thalamic degeneration. The latter was found in the dorso-medial and ventro-lateral thalamic nuclei on the same side. This

result is compared with the results of similar cortical lesions as produced by previous authors in animal experiments. The degeneration following lesions of the premotor area was more extensive than might have been expected from those experiments.

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# THE HIND FOOT OF *YOUNGINA* AND FIFTH METATARSAL IN REPTILIA

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In a paper on the Classification of the Reptilia (Goodrich, 1916) it was maintained that this Class is not a simple monophyletic group, but is composed of three main divisions: first a basal group of relatively primitive forms, the Protosauria, derived from some amphibian-like ancestor and retaining the complete bony roof of the temporal region of the skull; and two diverging branches, the Theropsida and the Sauropsida (Huxley's original term used in a restricted sense). The branch Theropsida (including the orders Mesosauria, Ichthyosauria, Plesiosauria = Sauropterygia, Pelycosauria, Dinocephalia, Dicynodontia, Theriodontia, and related forms) leads towards the Class Mammalia, and has only one temporal fossa pierced in the roof of the skull. Following Osborn (1903) these reptiles are often called the Synapsida. The branch Sauropsida (including the orders Eosuchia, Protorosauria, Rhynchocephalia, Squamata [placed here on the assumption that they have lost one or both of the temporal arches], Pseudosuchia, Phytosauria, Crocodilia, Pterosauria, Saurischia, Ornithischia) leads towards the Class Aves. In the Sauropsida two temporal fossae are developed, and they are often called the Diapsida (Osborn, 1903). The general conclusion that the Reptilia have diverged into these two main branches with synapsidan and diapsidan skulls had already been accepted by many authorities, and the chief object of my paper was to show that this conclusion was further strongly supported by evidence derived from the structure of the heart and of the skeleton of the hind-foot.

Of the sauropsidan specialization of the heart and bases of the aortic arches (further dealt with in greater detail in my later book: Goodrich, 1930) little need be said here, except that the mammalian heart and arches must have been evolved along very different lines from a more amphibian-like general structure. It is an important fact that the sauropsidan type of heart is fully developed in all living Reptilia, including the Chelonia.[1]

The other evidence comes from the tarsus and metatarsus, and concerns chiefly the peculiar modification of the fifth metatarsal which, in Sauropsida, tends to be shortened while its proximal widened end becomes strangely bent and 'hook-shaped' or 'hooked', as it may be called for short. It thus acquires

[1] So far as I am aware no palaeontologist has taken into account the vascular system when classifying the Reptilia, nor appreciated its great significance. Probably similar divergences could be found in other organs, such as the brain.

a very characteristic shape due to the development of a strong process extending medially (forwards) to articulate closely with the enlarged fourth distal tarsal at a level proximal to that of the other metatarsals, and an outstanding process at its outer angle (Fig. 1).

This modification of the fifth metatarsal is accompanied by the reduction of the fifth distal tarsal, and also is possibly related to the development of the mesotarsal articulation so characteristic of all the Sauropsidan reptiles and their offspring the birds. That the hook-shape of the fifth metatarsal was originally of functional significance seems highly probable, though no one as yet appears to have explained exactly what this function may have been. The detailed descriptions given by Perrin (1895) and Osawa (1898) of the musculature of the foot of *Sphenodon* throw little light on the problem.

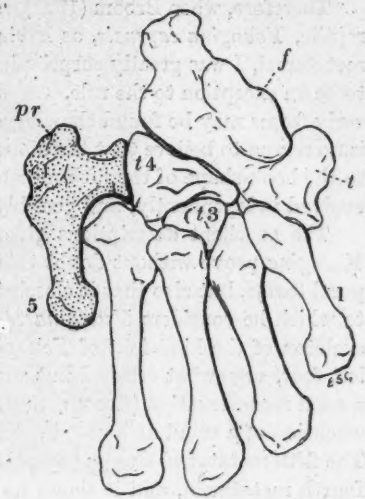



Fig. 1. Tarsus and metatarsus of *Varanus salvator*, Saur. Right foot, dorsal view. Fifth metatarsal shaded. *f*, articular facet for fibula on proximal fused tarsals; *pr*, outer process; *t*, articular facet for tibia; *t*3, third distal tarsal; *t*4, fourth distal tarsal.

It has been pointed out (Goodrich, 1916, p. 264) that 'the hook-shaped metatarsal does not seem to be closely related to any particular mode of life or method of progression, being essentially the same in reptiles of the most diverse habits'. It is seen in all groups of living reptiles with free outstanding limbs, is obvious in Lacertilia (Fig. 1), Chelonia, and *Sphenodon*, and can be traced in Crocodilia in spite of the great reduction of the fifth toe. Moreover, once acquired the modification seems never to be entirely lost, even when the foot becomes transformed into a paddle adapted for swimming—for instance in *Desmachelys* (Völker, 1913), and Mesosauria (Osborn, 1899). Further, the hook-shaped metatarsus was already developed not only in Triassic (*Howesia*, *Aëtosaurus*, etc.), but even in Permian times (*Palaeagama*, *Protorosaurus*).[1]

Lastly, a careful search of the literature and examination of all available specimens seems to warrant the following general statements: that the modified fifth metatarsal never occurs outside the Branch Sauropsida; that no

[1] The following list includes interesting genera of early fossil reptiles known to have a hooked fifth metatarsal: Eosuchia: *Palaeagama* (Broom, 1926); *Howesia* (Broom, 1906); *Noteosuchus* =*Eosuchus* (Broom, 1925). Protorosauria: *Protorosaurus* (v. Meyer, 1856; Seeley, 1887); *Sauranodon* (Lortet, 1892). Pseudosuchia: *Euparkeria* (Broom, 1913); *Aëtosaurus* (v. Huene, 1920). Rhynchosauria: *Rhynchosaurus* (Huxley, 1887; A. S. Woodward, 1906). Rhynchocephalia: *Homoeosaurus* (Lortet, 1892); *Champsosaurus* (Brown, 1913). Phytosauria: *Rhytidodon* (McGregor, 1909).

reptile living or extinct, and known for certain to possess a diapsid skull, has been found without it.[1] These facts are surely of significance.

Therefore, when Broom (1921) described the Upper Permian South African reptile, *Youngina capensis*, as having a diapsid skull but an unmodified fifth metatarsal, I was greatly surprised and interested. Here at last there seemed to be an exception to the rule. Of course it is to be expected that intermediate early forms may be found showing incipient stages in the modification. There is no reason to believe that the diapsid structure of the skull is directly related to the hook-shape of the fifth metatarsal. Doubtless these two specializations evolved independently, and possibly one considerably before the other.

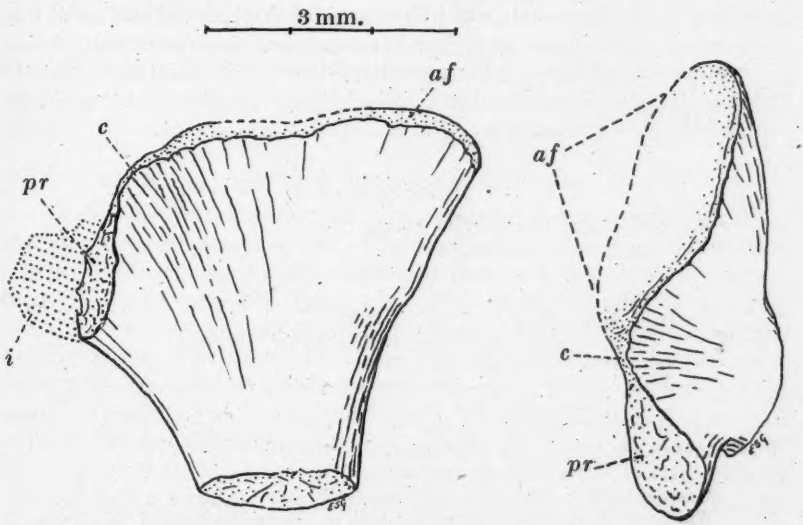
The excellent descriptions given by Broom (1922, 1924) of the skull of *Youngina* prove without doubt that it was not only provided with two temporal fossae, but also that it closely resembled the skull of *Sphenodon*, a genus to which he considers *Youngina* to be related. Broom's careful work on the skeleton of the hind foot of *Youngina* is almost entirely founded on a single left foot, somewhat crushed but sufficiently complete to provide material for a good reconstruction (Broom, 1921, Fig. 20). The tarsus is remarkable for the retention of a small fifth distal element attached to the usual enlarged fourth. The fifth metatarsal Broom says, 'is a long slender bone, nearly as long as the fourth metatarsal, and it shows no trace of the peculiar hooking. The upper end is expanded, and the outer process probably was attached to the fibulare by a ligament' (p. 152).

I am very grateful to Dr Broom for having sent me this precious specimen to examine. After careful scrutiny I am unable to agree with some of his con-

[1] Considering how striking is this character it is astonishing how little importance has been attributed to it by those authors who have attempted to classify the Reptilia. Williston mentions (1925) but does not insist on it. Watson (1917), although admitting that it is present in chelonians, rhynchocephalians, thecodonts, crocodiles, dinosaurs, and squamata, refrains from attributing much weight to it 'because it is difficult to believe that all these forms can have been derived from some advanced Cotylosaurian ancestor'. He suggests that it is perhaps an arboreal adaptation, which may have originated separately. But surely it is still more difficult to believe that this special form of fifth metatarsal has arisen independently so many times, and especially that the Chelonia should have had arboreal ancestors. Moreover, the Chameleons, probably the most specialized of all reptiles for arboreal life, are just those lizards in which the modification is least obvious!

Piveteau (1926), in his interesting description of the Permian reptiles of Madagascar, states that the fifth metatarsus of *Tangasaurus* is shortened and (at stage A) 'présente une forte dilatation de la têté proximale', but that at later stages 'sa tête supérieure n'est pas recourbée' although widened. Nor could I discern that it is distinctly hook-shaped in a large specimen Mr Parrington kindly allowed me to examine at Cambridge. The affinities of *Tangasaurus* are still uncertain since the structure of its skull is not fully known, and the evidence from the hind foot seems to be indefinite. Possibly we have here an early form in which the modification of the metatarsal is only beginning. Piveteau (1926) goes on to say that the modification of the fifth metatarsal cannot be considered as 'fondamental dans la classification des Reptiles. Son apparition sporadique dans les groupes les plus divers montre qu'on ne peut lui attribuer une pareille importance'. But, as a matter of fact, as indicated above, its distribution far from being sporadic is remarkably constant. It occurs in some degree not only in all Chelonia, but also in all 'Diapsida', and in these only so far as we know.

Fig. 2. Photographs of part of skeleton of left hindfoot of *Youngina capensis*, Broom, showing ventral surface of fifth metatarsal displaced, 5; it is outlined in black. 4, fourth metatarsal cut short distally. Enlarged.




Figs. 3, 4. Drawings of ventral and proximal views of fifth metatarsal of *Youngina*; showing, *af*, articular facet for fourth and fifth distal tarsals, *c*, constriction between it and, *pr*, broken outer process; *i*, impress of process on matrix. Concealed outline drawn in broken line.

clusions stated above. Fig. 2 is a photograph showing the fifth metatarsal as it lies somewhat displaced, and Fig. 3 is a drawing of the same bone. Its main shaft is broken short, and its original length can only be conjectured from an impress on the matrix. Tl fifth appears to have been considerably shorter than the fourth metatarsal. It is true that the expanded proximal end is not markedly hook-shaped, yet certain of its features seem clearly to indicate that it is to some extent modified in that direction. The proximal edge of the expanded head is subdivided by a constriction into an inner rounded elongated articular surface (Fig. 4), and an outer projecting process now partly broken away. The persistence of an impression on the matrix (Figs. 3, 4) shows that this process must have been of considerable size. While the articular facet seems to have been, as usual in the 'modified' type, closely connected with the large fourth distal tarsal (and also probably with the reduced fifth distal tarsal), the outer projection must surely represent the similar process so characteristic of a typical hook-shaped metatarsal. Such an outstanding process is not found on normal fifth metatarsals. The conclusion seems inevitable that the fifth metatarsal of this Upper Permian Eosuchian *Youngina* was, at all events to some extent, modified towards the hook-shaped type.

## SUMMARY

After discussing the importance of the modification of the fifth metatarsal as a constant feature in that branch of the Reptilia to which the name Sauropsida may be applied (and in which the diapsidan skull occurs) this metatarsal is described in *Youngina*, an Upper Permian Eosuchian from South Africa, hitherto considered to be of the unmodified type. It is maintained that the fifth metatarsal of *Youngina* shows distinct signs of modification towards the sauropsidan hook-shaped type.

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# THE TERMINATION OF OPTIC FIBRES IN THE LATERAL GENICULATE BODY OF THE RABBIT

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In continuation of our previous research on the lateral geniculate body of the monkey (Glees & Clark, 1941) and the cat (Glees, 1941), we have tried to obtain further information on the mode of termination of the optic fibres in the lateral geniculate body of the rabbit. Our observations are limited to the synaptic relation of the optic fibres with the geniculate cells, since sufficient information about the retinal projection on the lateral geniculate body has already been gathered by Loepp (1912), Brouwer (1923), and Overbosch (1927).

## MATERIAL AND TECHNIQUE

For both the normal and the experimental material, full-grown rabbits were used. In one case both optic nerves were cut, in six other cases the right optic nerve only. The material was fixed by immersion of the brain slices in formalin, to which 10 drops of pyridine per 100 c.c. of 10 % formalin was added. The method of injection of formalin-saline has been abandoned because it sometimes produced a dilatation of the vessels, including the capillaries, which gave a perforated appearance to areas with a dense capillary plexus. It also seems that too sudden a fixation has the effect of staining the cells in a silver impregnation unevenly and too dark a colour. Frozen sections were made, and were stained either with toluidin blue or with Hortega's impregnation for neurofibrillae and with the Bielschowsky-Gros method.

### *Normal histology of the geniculate body in the rabbit*

We shall concern ourselves here only with those normal features which are essential for understanding the changes resulting from this experiment. A definite arrangement in laminae, so easily observable in the monkey and cat, cannot be found here. The stratification of the geniculate body is caused by optic fibre bundles passing through the body towards the anterior corpus quadrigeminum. The nerve cells in the silver preparations are more or less of uniform appearance and of medium size. The characteristic large cells present in the cat geniculate body seem to be absent. A careful description of the cells as shown by the Nissl stain, and their arrangement in groups, was given by Rose (1935), while Cajal (1911) describes their appearance in the Golgi preparation and divides them into two groups—those with long axones and those with short axones. The suggestion has been put forward that the second of these types may serve as an intercalated neurone; on the other hand, according to O'Leary (1940), such cells may act as synchronizing agents. Cajal, using the

Golgi technique, describes the optic fibres of the newborn rabbit as ending in brush-like terminals; these terminal branches with no definite end formations are the so-called 'free endings'. In silver preparations from full-grown animals, dendrites and optic terminals form a very dense neuropil, and the terminal arborizations of optic fibres which stand out in Golgi preparations so clearly are undetectable in full-grown rabbits. With the use of an oil-immersion lens the individual nerve cells of the geniculate body are seen to be surrounded by a dense neuropil. After careful study we were able to find very fine terminal rings of the size of the nucleolus of a nerve cell in contact with the cell body and the dendrites (Pl. 1, figs. 1, 2). These rings or loops may appear in the form of an isolated end-formation, or grouped together and forming a *terminaison en grappe*. It is possible to detect up to ten such terminals in contact with the perikaryon (axo-somatic). There are also numerous terminals in contact with the dendrites, but an approximate estimate of the numbers related to the dendrites of one individual cell could not be made because it was impossible to stain all the dendrites of one cell with any certainty. However, the large number of terminals in synaptic relationship to the dendrites is proof of the existence of axo-dendritic contacts.

In order to ascertain whether these rings belong to the optic endings, and, if so, to study their mode of degeneration, we cut the optic nerve and let the animals survive for different time intervals.

### *Changes in the lateral geniculate body following the section of the optic nerve*

Exp. R 206. 2 days. No alteration can be obtained sufficient to prove the existence of any change from the normal geniculate body.

Exp. R 213. 3 days. Here both optic nerves were sectioned. When examined under medium power the general picture seems to be unchanged and the neuropil is of normal density; however, when an oil-immersion lens is used the fine terminal rings and *terminaisons en grappe* are seen to stain much more deeply, are more conspicuous, and are slightly enlarged as compared with those of a normal preparation. About one-third of the terminal rings are enlarged to twice their normal size. The nucleolus of the ganglion cell presents an easy standard for assessing this enlargement. Degeneration of terminal branches ending in these rings is not yet visible.

Exp. R 207. 4 days. At this stage the terminal rings have progressed considerably in their degenerative phase (Pl. 1, fig. 3). A greater number of terminals are now enlarged to twice their normal size, and the contour line is more deeply impregnated. The degree of degeneration gives almost all the terminals the capacity to stain more readily with silver, so that a fairly complete staining of the terminals is obtained. Another very characteristic sign at 4 days is that the thin fibres ending in a ring or loop become more conspicuously stained also. In normal preparations it is often difficult to trace the connexion of the fine rings and loops with terminal branches of the optic tract,

but at this stage of degeneration they become swollen and more deeply impregnated with silver.

Exp. R 209. 5 days. The characteristic feature of this stage of degeneration is that more rings become swollen; moreover, many are now transformed into little bulbs, a change which is accompanied by the disappearance of the lumen of the ring formation (Pl. 1, fig. 4). Each bulb is darkly stained and is about three times the diameter of the original terminal ring. The fibres ending in these bulbs are swollen but not yet disintegrated.

Exp. R 210. 8 days. The changes described in the previous experiments now become more generalized and more evenly distributed over the lateral geniculate body, though no sign of any disintegration of the terminal optic branches into fragments can be found.

Exp. R 212. 14 days. Exp. R 208. 15 days. There is no difference in the changes shown in these two stages of degeneration, and they may therefore be considered together. A few terminal fibres ending in enlarged rings are still to be found at this stage, together with others ending in bulbs. The first phases of fragmentation of terminal fibres and their disintegration can now be seen. The capacity for staining at this phase is hindered by the widespread demolition taking place in the myelin sheath, where the debris of degenerated myelin gives a diffuse yellowish colour to the picture and makes it difficult to analyse in much detail.

Exp. R 211. 75 days. Those parts of the geniculate body which are concerned with relaying impulses from the cut optic nerve show the following changes (Pl. 1, fig. 5). Neither terminal rings nor bulbs of normal or pathological condition are present. A great deal of the neuropil normally present is missing, but there are still fibres in the stage of fragmentation to be seen, which makes it possible to reconstruct to some degree the normal pattern of the optic terminals. Optic fibres of larger diameter in the optic tract are still visible in various phases of degeneration. The resorption of axonic material seems to be considerably slower than that of the myelin products.

## DISCUSSION

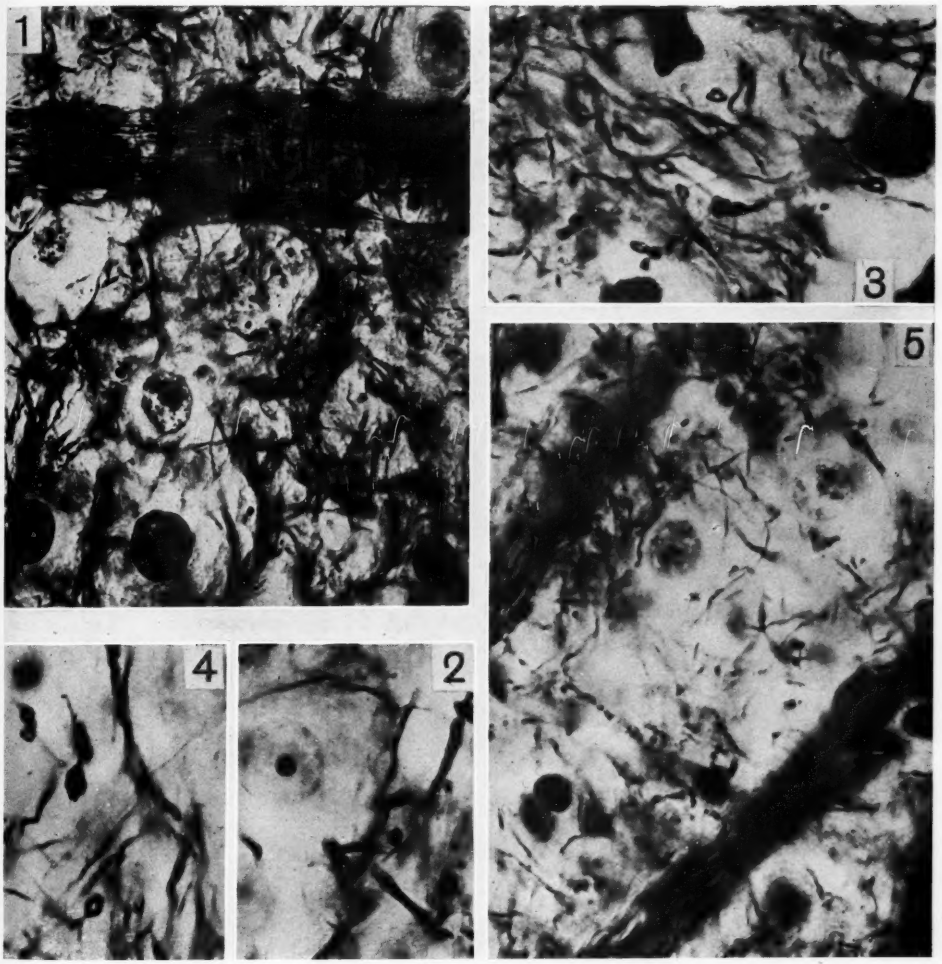
In the normal lateral geniculate body of the rabbit we find numerous terminal rings and loops in contact with the nerve cell bodies and their dendrites. This terminal apparatus is even more easily demonstrated in the rabbit than in the cat or monkey. After section of an optic nerve the terminals show changes which have previously been observed in our experiments on the optic terminals in the monkey and cat. It is therefore concluded that at least a great proportion, if not all, of the optic fibres in the rabbit end in a ring or loop-like end apparatus. These terminal loops or rings undergo a characteristic degeneration. The number of terminals in contact with the cell body is estimated at approximately ten, but it has been found impossible to give any estimate for terminals related to dendrites because the dendrites either did not stain completely or did not stain at all; however, the presence of terminals in the

neuropil makes it certain that a great number are related to dendrites. With the technique employed it proved impossible to stain the whole arborization in several of the optic axones, and therefore no statement can be made with certainty about overlap, but judging from the Golgi preparations described by Cajal and by our own experiments with the cat it may be assumed that overlap does exist.

A confirmation of the view that the optic terminals react in a characteristic manner after they have been separated from their cells of origin in the retina can be found in a paper by Cattaneo (1923). This author cut the optic nerve in the chicken and rabbit and observed the reactions in the tectum opticum and (to a lesser degree) those in the geniculate body. He found that, several days after section of the optic nerve, very fine fibres in the geniculate body and the tectum opticum end in little rings and bulbs; these gradually disappeared after a fortnight. These experiments were carried out in Rossi's laboratory at a time when the question of the regeneration of nerve fibres was still very much a subject of controversy. It is understandable, therefore, that Cattaneo considered the phenomenon observed as a sign of an attempt at regeneration in the optic terminals following separation from their cells of origin. Cattaneo accepted Cajal's statement that the optic fibres have only free endings in the lateral geniculate body, and for this reason he did not give sufficient consideration to the normal histology of the geniculate body which might have suggested that the rings and bulbs he observed were due to pathological changes taking place in a normal end apparatus. In his time terminal changes in axones showing rings or bulbs were considered to prove a tendency towards regeneration, even though it seems unlikely that fibres lacking connexion with their trophic centres, such as the central part of a cut optic nerve, should be able to regenerate.

There is a certain amount of evidence to indicate that it may be rather a general phenomenon of the nervous system that terminals do not end freely but have a definite end apparatus. The classical example of a definite end apparatus is in the spinal cord; here, with the method described above, the ventral horn cells are found to be covered with terminal rings which are partly filled with a very fine neurofibrillar network. Material from the spinal cord, fixed and stained in the same way as that from the geniculate body, was used to test our own methods. The terminals observed in the spinal cord were indeed found to be identical with those of the geniculate body; similar terminal rings in the nuclei of the cranial nerves could also be detected. It is now generally accepted that the motor cells and relay neurones of the central nervous system receive terminal boutons (Hoff, 1932; Gibson, 1937; Phalen & Davenport, 1937; Schimmert, 1938; Barr, 1940). It is therefore not surprising that the geniculate cells, acting in the capacity of relay neurones, also form their synapse with the optic fibres by terminal rings.

The terminal apparatus of the sympathetic ganglia shows similar changes after the connexion with its afferent system has been severed. Fedorow &



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Matwejewa (1936/1937) describe definite terminal rings ending on the cell body and dendrites of the sympathetic ganglion cells. Their findings support our own observations, and I should like to quote from them.

'La modification de dégénération que subissent les fibres nerveuses et leurs terminaisons par suite de la section, apparaissent tout d'abord, dans les ramifications terminales des axons, c'est à dire, dans notre cas, dans les appareils péricellulaires. Le premier symptôme de la dégénération se traduit par l'intensité croissante avec laquelle s'imprègnent les disques terminaux. Leur structure réticulaire caractérisant un état normal devient homogène. Vers ce temps les disques se trouvent gonflés. . . . Les disques gonflés se laissent observer beaucoup plus longtemps que les fibres grêles de l'appareil péricellulaire pendant un délai assez long.'

A similar observation was made by de Castro (1936). An extensive discussion and further experiments on terminal boutons in the sympathetic ganglia can be found in a recent paper by Gibson (1940).

The results obtained on the degeneration of the terminal apparatus in the spinal cord and sympathetic ganglia confirm our own observations on the geniculate body of the monkey, cat and rabbit, namely, that terminals become more clearly visible after the efferent fibres have been sectioned. The terminals (or at any rate their debris) persist for a much longer period than might be expected.

In conclusion, it seems advisable to stress the difference between traumatic degeneration and that taking place in the terminal boutons. Traumatic degeneration is confined to the neighbourhood of the lesion and has been studied and described in detail by Cajal (1928). Degeneration in terminal boutons takes place at a distance from the lesion, in the terminal arborizations of the injured fibre tract, and may be termed 'terminal degeneration'. The latter can be easily demonstrated in those terminal arborizations of fibre tracts which end in a definite end formation (the rings and 'end feet' of Held). It is probable that this terminal degeneration can occur in free terminals also. For example, Cajal (1928) gives a description of the baskets of Purkinje cells on p. 628 of vol. 2 of his book *Degeneration and Regeneration of the Nervous System*. These basket fibres, which are described as free terminals, end in terminal clubs in this picture. Cajal made this observation after experimental injury to the cerebellum in young animals. It can therefore be concluded that this terminal degeneration occurs in the terminal arborizations both of fibres which end freely and of those which have definite end formations. The changes shown by widespread degeneration are clear enough to demonstrate the final destination of a fibre tract or the synaptic connexions of neurones.

## SUMMARY

1. The optic fibres in the rabbit end in the lateral geniculate body in special end formations, i.e. fine terminal rings.

2. After section of an optic nerve these optic terminals undergo characteristic degeneration.

3. The number of synaptic contacts with the cell body (axo-somatic) is estimated at approximately ten.

4. Synaptic relations with the optic fibres are also established by axo-dendritic contacts.

5. Attention is drawn to the desirability of distinguishing between 'traumatic' and 'terminal' degeneration in the study of degenerative changes in nerve fibres.


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## EXPLANATION OF PLATE 1

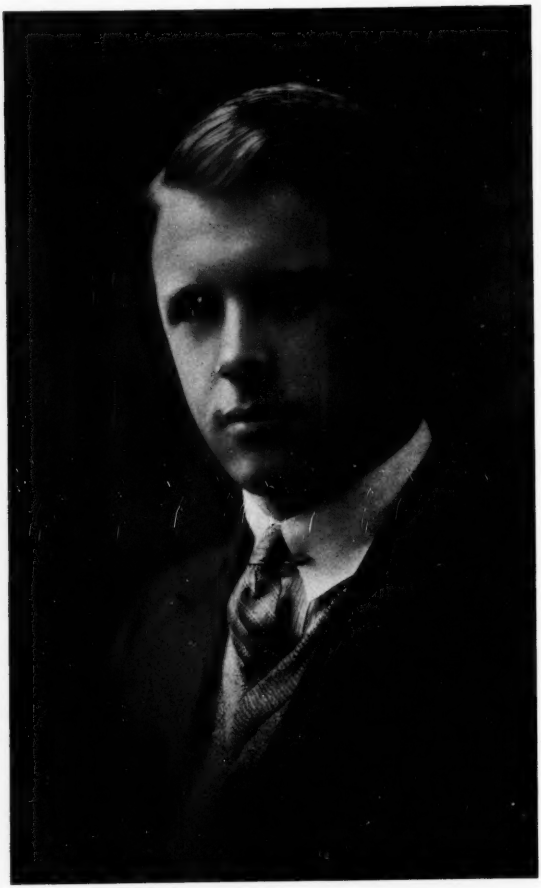
Fig. 1. The normal appearance of the lateral geniculate body of the rabbit. In the middle of the picture the surface of one cell has been brought into focus, showing that it is covered by numerous optic terminal formations. × 820.

Fig. 2. A normal optic terminal ring is seen in contact with a dendrite. Compare diameter of the ring with the diameter of the nucleolus of the adjacent ganglion cell. × 1640.

Fig. 3. Exp. R 207 (4 days). The optic terminals are in process of degeneration. They are enlarged and their connecting fibres are clearly visible. × 1640.

Fig. 4. Exp. R 209 (5 days). At this stage of degeneration the lumen of the terminal rings begins to disappear and becomes replaced by a bulb-like formation. × 1640.

Fig. 5. Exp. R 211 (75 days). The neuropil has lost its normal density (cf. Fig. 1). The terminal optic fibres which still persist are in a fragmented condition. No terminal rings are visible. × 820.



JAMES HUGO GRAY
1909–1941

UNIV. OF MICH.

# IN MEMORIAM

## JAMES HUGO GRAY, 1909–1941

The sudden and untimely death of Hugo Gray on 20 December 1941, was a great shock, not only to his personal friends but also to all those who have at heart the interests of anatomical science. For, already in a short career, he had made several highly important contributions to his subject, and his future career as a productive worker seemed assured.

Gray was born in Adelaide in 1909, and there he spent his childhood and his school days. His industry at this time was rewarded by a number of school prizes and by a scholarship which enabled him to proceed to the University. Here, as a medical student, he came under the personal influence of the late Prof. Woollard in 1929, and assisted in research studies while still an undergraduate. It was this experience which determined his career as an anatomist. He took his medical degree in 1932, and he was elected Everard Scholar for obtaining the first place in the final examinations of his year.

With the intention of fitting himself for the career of an anatomist, Gray accepted the post of Physical Anthropologist in four University expeditions to Central Australia between the years 1930 and 1933. After that he worked for a year as Resident Medical Officer at the Adelaide Hospital. He was then appointed Demonstrator in Anatomy at the University of Adelaide. Urged by the inspiration of his early work, he determined if possible to continue his studies under his old teacher, Prof. Woollard, who had meanwhile been appointed to the Chair of Anatomy at St Bartholomew's Hospital Medical College in London. Accordingly he took the bold step of himself coming to England. Barely able to afford his passage, and quite uncertain whether he would find a post when he arrived, he reached London in 1935. He was rewarded for his enterprise by being appointed to a Cancer Research Fellowship. In 1936 he won the Corrie Prize for Anatomical Research at St Bartholomew's Hospital, and by now he had fully established himself as a promising young anatomist. In 1936 he accompanied Woollard to the Anatomical Institute of University College, London, where he was appointed Demonstrator. Finally, in May 1941, at the remarkably early age of 32, he was elected to the Chair of Anatomy in the University of London at St Mary's Hospital Medical School.

Gray's interests were mainly in experimental anatomy, and in recent years he had concentrated his attention on the capacity for growth and regeneration of lymphatic vessels, and on the reaction of lymphatic tissue to a variety of pathological conditions. The results of these studies, which were based on

exceptionally critical observations as well as on an ingenious experimental technique, were published in the ***British Journal of Surgery*** and in the ***Journal of Anatomy***. The clinical significance and importance of this work will be apparent to those who are acquainted with it. Gray also had quite a wide knowledge of comparative anatomy, and at the beginning of his career he had published several anthropological papers dealing with the Australian aboriginal.

As a teacher, Gray's qualities received full recognition. His methods were founded on the principle that anatomy should be taught primarily as a laboratory science, and that it is far more important that medical students should be well grounded in the principles of structural organization than that they should be required to clog their minds with those topographical minutiae which have little practical and no educational value. On the other hand, he by no means neglected the teaching of topographical anatomy, but he held that this should be confined as far as possible to those details which would later be found necessary for the understanding of general medicine and surgery. In his short time at the Chair of Anatomy at St Mary's Hospital Medical School, Gray had earned the respect of his colleagues for his energy and initiative in the organization of his new Department along progressive lines.

To those who did not know him well Hugo Gray appeared of a shy and retiring disposition. This, however, was but an expression of a natural modesty, for in reality he had a somewhat aggressive character to the extent that he would brook no opposition to the attainment of those aims which he believed to be worthy or necessary for the purpose of his work and the advancement of his subject. He was dominated by two major motives—a deep sense of loyalty to his friends and colleagues, and an intense desire to secure proper recognition of anatomy as a vital and progressive science. His anatomical colleagues mourn Gray's death not only because of the personal loss but as well because they will sadly miss the stimulus of his collaboration in the progressive development of anatomical teaching and research.

Prof. Gray leaves a widow and three young children, and to them we extend our most sincere sympathy.

## List of Publications by Prof. James Hugo Gray

1933

'Some pathological lesions seen in Central Australian aborigines' (with J. B. Cleland). *J. Trop. Med. Hyg.* **36**, no. 9.

1934

'Pathological lesions in natives of Central Australia' (with J. B. Cleland). *J. Trop. Med. Hyg.* 6 Jan.

'Pathological lesions met with amongst the aborigines in the Musgrave Ranges, South Australia' (with J. B. Cleland). *J. Trop. Med. Hyg.* **37**, no. 2.

1935

'Preliminary note on the mast cells of the human pituitary and of the mammalian pituitary in general.' *J. Anat., Lond.*, **69**, 153.

'The hair tracts of the Australian aboriginal.' *J. Anat., Lond.*, **69**, 206.

1936

'Physical anthropology of aborigines of Central Australia. Part I' (with T. D. Campbell and C. J. Hackett). *Oceania*, **7**, no. 1.

'Physical anthropology of aborigines of Central Australia. Part 2' (with T. D. Campbell and C. J. Hackett). *Oceania*, **7**.

'Observations on the teeth of Australian Aborigines' (with T. D. Campbell). *Austr. J. Dent.* **40**, 290.

1937

'The lymphatics of the stomach.' *J. Anat., Lond.*, **71**, 492.

1939

'Relation of lymphatics to the spread of cancer.' *Brit. J. Surg.* **26**, 462.

1940

'Studies of regeneration of lymphatic vessels.' *J. Anat., Lond.*, **74**, 309.